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Territorial behavior of the Red Admiral Butterfly, *Vanessa atalanta* (L.) (Lepidoptera: Nymphalidae)

Royce Justin Bitzer
Iowa State University

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**Territorial behavior of the Red Admiral Butterfly,
Vanessa atalanta (L.) (Lepidoptera: Nymphalidae)**

by

Royce Justin Bitzer

**A Dissertation Submitted to the
Graduate Faculty in Partial Fulfillment of the
Requirements for the Degree of
DOCTOR OF PHILOSOPHY**

Department: Zoology and Genetics

Interdepartmental Major: Ecology and Evolutionary Biology

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

For the Interdepartmental Major

Signature was redacted for privacy.

For the Major Department

Signature was redacted for privacy.

For the Graduate College

**Iowa State University
Ames, Iowa**

1995

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This dissertation is dedicated to Henry F. Swanson, Extension Director Emeritus of Orange County, Florida, who has patiently observed over 4,000 initial arrival times of Red Admiral Butterflies during the past 18 years, and who shares my interest in and understanding of their behavior.

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DISSERTATION ABSTRACT

This study of territorial behavior in the nymphalid butterfly *Vanessa atalanta* examines a number of behavioral and climatic factors shaping how, when, and for how long they maintain territories during the late afternoons of late spring and summer. Territorial *V. atalanta* males were observed on the Iowa State University campus from early April/early May to late August/early September from 1987 to 1992 on a total of 224 days. Microclimatic conditions were simultaneously recorded with automatic datalogging equipment. Males started territorial activity later on warmer days and when the ground was cooler, under all types of cloud cover. Although body temperature depends most strongly upon solar radiation, ambient and surface temperatures were more strongly correlated with territorial start time. *V. atalanta* males therefore do not always start territorial behavior at times when they can reach optimal body temperatures by dorsal basking.

The time of end dance, the last interaction between a *V. atalanta* territory occupant and an intruder, correlated with both ambient temperature and interaction frequency during the territorial period. Vagrant *V. atalanta* males stopped flying later on warmer days, and when mean interaction frequency was higher, and when wind velocity was higher. Flying *V. atalanta* males were limited by a lack of radiant energy on cooler days. On warmer days, however, oncoming darkness at twilight, rather than lack of radiant heat, seemed to limit the activity period.

End time, when *V. atalanta* males leave their territories, correlated most strongly with end dance time. Butterflies also leave later on warmer days, probably due to the fact that end dance time also varies with T_a . Occupants also

leave later when interaction frequency is higher. Butterflies leave considerably earlier on cloudy days than they do on sunny ones. This may be related to either surface temperature or diffuse solar radiation levels, or both. These three studies together yielded a climate space model showing the territorial activity period under various conditions.

Behavioral and climatic factors affecting outcome and duration of territorial interactions were also examined. Larger occupants which chased during an interaction were more likely to win. Occupants also tend slightly to lose their territories to intruders more often when the air temperature is warmer. Interactions are shorter on warmer days and when the two contestants are more disparate in size. Strategic factors more strongly affected whether a butterfly won, lost, or tied in an interaction than did climatic factors such as ambient temperature.

GENERAL INTRODUCTION

Dissertation Organization

The subject of this dissertation is the territorial behavior of the Red Admiral Butterfly, *Vanessa atalanta* (L.) and how it depends upon various climatic and behavioral factors. One published manuscript and three manuscripts to be submitted for publication make up a large part of this work.

Section I, including the first three chapters, concerns the daily activity schedule of territorial behavior and the extent to which it depends upon both climatic factors and population density of vagrant male butterflies invading territories. Each discusses factors correlated with shifts in butterfly behavior occurring just before and during the territorial activity period. Chapter 1 describes and models how climatic factors such as ambient and substrate temperatures, cloud cover, solar radiation, and wind velocity correlate with *start time*, when *V. atalanta* males set up their territories each afternoon. It also examines whether or not this time is correlated with early interaction frequency. Chapter 2 discusses how the time of the last territorial interaction, or *end dance*, correlates with the climatic factors above and with the interaction frequency during the territorial period. Chapter 3 discusses factors and events correlated with *end time*, the moment when butterflies fly up and out of their territories to seek roosts for the night in high tree branches.

In Section II, the fourth and final chapter analyzes *V. atalanta* territorial contests. It examines behavioral and climatic factors which influence the outcome and duration of interactions, and shows which butterflies under what conditions are more able to occupy and defend a territory. It also compares the

relative importance of factors such as male size, status, and chase position with that of climatic factors such as temperature and cloud cover.

These manuscripts are preceded by a general introduction that includes this explanation of how the dissertation is organized, then describes *V. atalanta*, its range, habitat, seasonal migration patterns, and the details of its territorial behavior. Then follows a review of butterfly territorial behavior and butterfly thermoregulation as it relates to the period of territorial activity, and an introduction to how butterflies might resolve territorial contests. The general introduction concludes by describing the general observational procedures of this study. The final section following the manuscripts is a general discussion that summarizes how both microclimatic and behavioral factors affect the timing and intensity of territorial behavior. References cited in the general introduction and general discussion follow the general discussion.

The Red Admiral Butterfly, *Vanessa atalanta* (L.)

Description, Range, Habitat, and Seasonal Migration Patterns

The Red Admiral, *Vanessa atalanta*, is a common and cosmopolitan Holarctic nymphalid butterfly. It inhabits North America from central Canada through the Mexican highlands to Guatemala (Opler, 1992). Typical habitat is rich, moist bottomland woods containing larval host plants such as stinging nettle (*Urtica dioica*) and false nettle (*Boehmeria cylindrica*). *V. atalanta* is typically found in sunlit forest openings or margins (Opler and Krizek, 1984), often in or near stream courses; in moist fields, in city parks, and on ridge tops (Opler, 1992). The dorsal side of the wings is dark brown to black. The forewing has small white apical spots and a prominent red-orange median band, and the

hindwing has a red-orange marginal band. *V. atalanta*'s wing span varies from 58 to 76 mm (Opler, 1992); the male forewing length ranges from 2.6 to 3.3 cm (mean = 3.1 cm) (Opler and Krizek, 1984). Although *V. atalanta* shows little morphological variation over its geographic range, it has distinct summer and winter forms. The summer form is larger and brighter, with an interrupted forewing band, whereas the winter form is smaller and duller in color (Opler and Krizek, 1984). *V. atalanta* is double-brooded throughout most of its range (Opler and Krizek, 1984); it is single-brooded in the northernmost United States and Canada, and triple-brooded in the southern states. In Iowa, *V. atalanta* is active from mid to late April to late September or early October. *V. atalanta* is seasonally migratory (Opler and Krizek, 1984; Opler, 1992). It probably cannot survive colder winters in the northern part of its range (Opler, 1992), although Shapiro (1974) reports that adults hibernate successfully as far north as New York. It overwinters in the southern states, including south Texas (Opler, 1992) and Florida (Swanson, 1979).

Perching and Territorial Behavior

Male butterflies adopt one of two general strategies when seeking mates (Scott, 1974). Patrolling species search for females by flying over a broad area, whereas perching species perch on rocks, trees, shrubs, hilltops, or on flat ground and wait for females to fly by. Many of the fast-flying, relatively short-winged nymphalids are perching species (Joy, 1902; Shields, 1967; Baker, 1972; Dimock, 1978; Bitzer and Shaw, 1979; 1983; Swanson, 1979; Alcock, 1984; 1985; Brown and Alcock, 1991; Rutowski et al., 1991). Some of the lady butterflies of the genus *Vanessa*, including *V. atalanta*, are perching or territorial (Shields,

1967; Dimock, 1978; Swanson, 1979; Bitzer and Shaw, 1979; Alcock, 1984; Opler and Krizek, 1984; Brown and Alcock, 1991).

Bitzer and Shaw (1979) and Swanson (1979) have described the territorial behavior of *V. atalanta*. As is typical of *Vanessa* sp. generally (Opler and Krizek, 1984), *V. atalanta* males hold territories from mid to late afternoon to around sunset. Different males consistently occupy the same territories on different afternoons and even from year to year. The territories themselves are roughly elliptical in shape, varying from 8 to 24 m long and 4 to 13 m wide. They are typically located in small open spots within a ring of trees which is open to sunlight on the west side, or on west facing walls or embankments flanked by a partial circle of trees. Their major axes often are oriented toward or lie along linear visual features such as sidewalks, trails, and rows of trees. Each territory has a core area, an area common to a territory mapped on successive days. The area peripheral to the core area sometimes varies with different territorial occupants.

Each territory contains one to several frequently-used resting spots within its core area. Many occupants consistently perch upon the same spots, which are usually on the ground (sidewalks, rocks, or patches of bare sunlit ground), on sunlit walls of buildings, or, less often, on a bush or low branch of a tree.

V. atalanta males define their territorial boundaries by patrolling within their territories ca. 7 to 30 times/h (Bitzer and Shaw, 1979). During a single patrol, a male traces a flight path two to six times in a period of 5 to 60 s before returning to his perch. They usually patrol about 1.5 m above the ground, or may patrol along walls in a winding fashion.

Territory occupants defend their territories by trying to out-fly and out-maneuver intruders and so drive them away. Interaction frequency ranges from less than one to over 100/h, but is commonly between 10 and 15/h (Bitzer and Shaw, 1979). Intruders typically enter a territory along specific flight routes, flying from 0.30-1.70 m above the ground. The resting or patrolling occupant then flies up or changes course, rushes at the intruder from underneath, and sometimes hovers above the intruder for 1 to 2 s before chasing it along an erratic path 1-2 m above the ground for 3 to 20 s. Then the occupant closes to within 30 cm of the other and begins chasing it along one to seven turns of a helical path, 4-9 m in diameter, ascending 10 to 18 m to treetop level. The occupant then drives the intruder over the treetops, breaks off the chase, and drops back into its territory (Bitzer and Shaw, 1979). This helical flight allows the occupant to chase intruders a relatively great distance upward without moving a large horizontal distance from its territory. If a third butterfly attempts to usurp the territory, the occupant often breaks off the chase and drops down to intercept the new intruder. At the same time, the first intruder may become disoriented in the overhead branches and lose sight of the territory.

Some territories are considered more preferred or optimal than others because they are occupied more frequently from day to day. The highest rates of occupant-intruder interactions occurred in optimal territories. Such competition occasionally resulted in two or more males claiming the same territory. When more than one butterfly rested in a territory, any occupant which flew up, presumably while attempting to patrol, was immediately chased by another occupant. The results of such competition were 1) establishment of an adjacent territory; 2) splitting of a territory into two smaller territories; 3) intermittent

chases occurred until all butterflies flew away at the end of the territorial period; 4) one or more butterflies were driven off, and 5) the smaller or smallest butterfly stealthily perches in an out-of-the-way location near the territorial boundary and flies up only in response to incoming vagrants.

Territorial Behavior And Thermoregulation Of Butterflies

Although many observers and experimenters have studied either the reproductive strategies or the thermoregulatory behavior of butterflies, relatively few had examined in great detail the relationship between the two before I began this study. For this reason, I decided to study a number of behavioral and climatic factors which shape how, when, and why *V. atalanta* males maintain territories during the late afternoons of late spring and summer.

I examined in this study both behavioral and climatic factors which correlated with when *V. atalanta* males established their territories, how long they stayed there, and when they left to go to roost for the evening. I also studied how both behavioral factors, such as contestant size, chase position, and prior occupancy of a territory, and climatic factors, such as ambient temperature (T_a), affect both the outcome and the duration of territorial interactions, and which of the two types of factors is more important.

The study of butterfly territorial behavior is one of the few types of behavioral studies in which the effects of both reproductive strategies and climatic factors have been used when developing models. This has been done because butterflies are such obvious ectothermic sun-baskers. Because of the potential payoffs of this approach, biologists are studying more and more the

role of climatic factors with respect to the reproductive strategies of other animals, including endotherms.

Factors Affecting Daily Territorial Activity Schedule

Two factors determine whether butterfly males of the same or different species perch or patrol, strategies for locating mates and climatic factors which affect body temperature (Dennis and Williams, 1987; Rutowski, 1991; Scott, 1974; Wickman and Wiklund, 1983; Wickman, 1985a; 1985b; 1988). Non-territorial males that locate all, or almost all, females while flying (patrolling), may only perch when climatic conditions result in body temperatures too low to maintain flight. Vielmetter (1958) described a "change of state" in which the non-territorial nymphalid *Argynnis paphia* switched between continuous flight and stationary basking according to an inverse relationship between ambient temperature (T_a) and solar radiation. When the air temperature was low, males flew only when the sun, and therefore solar radiation, was high. On warm days, males could fly longer and not perch until the sun was low. Various combinations of these two factors yielded a critical body temperature (T_b) of 34.2° C, at which butterflies would switch from one behavior to another. Vielmetter (1958) also estimated a lower critical T_b of 23.4°C, at which butterflies left their perches and flew up into branches to roost for the night.

In species such as the satyrids *Pararge aegeria* and *Coenonympha pamphilus*, males patrol for females at warmer temperatures and defend sunlit patches at lower temperatures while waiting for females to alight and bask (Wickman and Wiklund, 1983; Shreeve, 1984; Wickman, 1985a). These satyrids move from sun patch to sun patch and the period during which they defend

sunlit patches varies with the change in air temperature. There is no specific time at which they begin territorial activity. Instead, they perch throughout the day, and the density of perched males peaks during times when conditions are thermally most favorable.

In other territorial species, such as *Aglaia urticae* and *Inachis io* (Baker, 1972), *Vanessa atalanta* (Bitzer and Shaw, 1979; Swanson, 1979; personal communication), and *Lasiommata megera* (Dennis, 1982), males establish territories in predictable areas, apparently defined by certain visual features, at a specified time and duration each day. In these species, males may fly up from perches or from intermittent patrols within their territories to intercept females flying through the territories. Like zeitgebers of biological rhythms, climatic factors apparently modulate when territorial behavior begins and ends and the duration of patrols.

In an earlier study of *V. atalanta* (Bitzer and Shaw, 1979), I noticed that *V. atalanta* males began territorial activity later as the days became warmer. Shields (1967) observed that males of four hilltopping *Vanessa* species, including *V. atalanta*, started perching later on warm days than on cooler ones. Shields' graphed data indicated that *V. atalanta* males start territorial behavior an average of 8.74 min later with each 1° C increase in air temperature. Brown and Alcock (1991) and Swanson (1979; personal communication) showed that the daily territorial period of *V. atalanta* varies seasonally. Both the nymphalid *Chlosyne californica* (Alcock, 1985) and the lycaenid *Strymon melinus* (Alcock and O'Neill, 1986) showed both temperature-related and seasonal changes in the times they began territorial behavior each day. In his study of *Pararge aegeria*, Shreeve (1984) found that patrol duration depended upon air temperature

whereas perching duration depended upon solar radiation and basking site temperature. Wickman (1988) suggested that *Lasiommata megera* males often had to trade off between choosing an optimal perch temperature or an optimal T_a for flight.

In this study, I have examined the effect of a variety of climatic factors on territorial start time, i.e., when males switch from flying to territorial perching, of the red admiral, *Vanessa atalanta*. Most investigators have examined one or a few climatic conditions at times when butterflies were either patrolling or perching; a few, such as Shields (1967), Dennis and Williams (1987), and Brown and Alcock (1991) have examined the effect of one or a few conditions on the moment of transition between the two strategies. I am studying the effects of air temperature, solar altitude, solar radiation, substrate temperature, wind speed, wind direction, perch site, intruder and interaction frequency, and cloud cover upon territorial start and end time and time of last interaction (end dance). I am closely examining and modeling a variety of factors which may affect when *V. atalanta* males begin and end territorial activity (= territorial start and end times), and have found that *V. atalanta* males' decisions to both start and end territorial activity for the day are more complex than the simple "change of state" responses which Vielmetter (1958) describes.

Factors Affecting Contest Duration and Outcome

Among animals in which individuals can inflict injury or in which strength matters in some other way, contestants decide to continue or to give up fighting based on cues such as size or weight which affect the probable outcome of a contest. In occupant-intruder interactions, occupants tend to be more successful

than intruders (Maynard Smith and Parker, 1976; Leimar and Enquist, 1984), partly because strong individuals tend to hold valuable resources. This in turn will select for role-dependent strategies, since an opponent's role conveys information about its resource-holding potential (RHP). Residents should use more persistent strategies than intruders, since they have more to lose (Maynard Smith and Parker, 1976; Leimar and Enquist, 1984).

Another reason that a territorial butterfly may be more successful is that butterflies are visually-oriented animals which become familiar with the landmarks of their territories after having occupied them for a time (Baker, 1972; Dennis, 1982; Alcock, 1984), and thus have an advantage over newly-arrived intruders, at least in the initial interactions (Baker, 1972).

Thus we expect residents to be more successful even in contests between equally-sized individuals, and in interactions between individuals of unequal size, small occupants should defeat larger intruders more often than small intruders drive off larger occupants (Rosenberg and Enquist, 1991).

The position of leading vs. chasing during an interaction may also be important to outcome. Typically each butterfly tries to jockey for a position above and behind the other before the main chase begins (Baker, 1972), so chasing rather than leading seems to be the dominant position. There is also a question of whether position is a cause or an effect of outcome.

Microclimatic factors also affect the duration and possibly the outcome of territorial interactions. Wickman and Wiklund (1983) found that *P. aegeria* interactions were shorter at higher ambient temperatures. Wickman (1985a) found that the interactions of *C. pamphilus* lasted longest in the morning and the afternoon when the air was cooler and males showed the greatest tendency

to perch, and were shortest at mid-day when males are more likely to patrol in search of mates. Wickman and Wiklund (1983) suggest that sun-patch-based territories become less valuable to *P. aegeria* at warmer temperatures because females then have less need to go to sunny patches to bask. Interactions should thus become shorter either because occupants strive less to keep their territories, or because intruders strive less to capture them, or a combination of both.

Other factors such as solar radiation and substrate temperature (Shreeve, 1984; Wickman, 1988) may also affect interaction duration by imposing thermal constraints upon flight or by affecting the attractiveness of perching or territorial behavior as a strategy.

One question which needs closer examination is whether or how much the duration of a territorial interaction affects the likelihood that an occupant will win. Baker (1972) found that for the nymphalid butterflies *Inachis io* and *Aglais urticae*, occupants were more likely to drive off intruders if they spent more time chasing intruders further from the territory (at increasing risk of not returning before the next intruder arrived).

Our study parallels Rosenberg and Enquist's (1991) study of the effects of size and residency upon the outcome of *Limenitis weidemeyerii* interactions, as well as examining some microclimatic effects. It is also the first to examine the relative importance of strategic and microclimatic factors in determining both the outcome and duration of interactions, and finally examines whether or not interaction duration is related to outcome in *V. atalanta*. This constitutes a critical test of Wickman and Wiklund's (1983) hypothesis. If occupants do yield their territories more readily to intruders on warmer days, yet interaction

duration does not affect or reflect the extent to which occupants do so, the idea that duration is a measure of a male's interest in keeping a territory becomes questionable.

General Observation Procedures

Butterflies were observed on the Iowa State University campus during the territorial season, which lasts from late April or early May to late August or early September. I chose territorial sites which were occupied nearly every day, but rarely by more than one male at a time. Most of my observing was done in two optimal [most frequently occupied (Bitzer and Shaw, 1979)] territories. One territory was 13.1 x 8.2 m with its long axis parallel to a sidewalk running east-west through a ca. 15 x 15 m partially sunlit spot open to the west and bounded on the other three sides by one large and five medium-sized trees. The other, located 26 m to the northeast, was a 9.1 x 6.7 m area beside and on a partially sunlit wall flanked by the large tree and one of the medium-sized ones. Sunlight falls in both areas most strongly before 1600 hr CST, then becomes patchier, and is gone by 1910-1930 hr.

All event times were recorded to the nearest second (CST) with a digital quartz clock/stopwatch set to WWV time signals, and converted to four-place decimal equivalents.

Ambient temperature (T_a) was recorded with a shaded, aluminum-encased thermometer suspended 75 cm above the lawn surface. This was approximately the altitude of the lowest-flying incoming intruders. T_a was recorded at 5-10 min intervals before start time, within 1 min afterward, and at 10-20 min intervals thereafter, depending upon the activity level of the butterflies. A 10-20

min interval was the shortest period during which the thermometer showed a noticeable drop (0.1°C), except on days with broken cloud cover. We let the thermometer equilibrate at least 10 min before reading it.

T_a was also recorded at altitudes of 13, 75, and 160 cm with three white-tube shielded 24 AWG copper-constantan thermocouples attached to a Campbell Scientific 21X Micrologger. The three thermocouples read within 0.05°C of each other in water (at both 0° and 45°C), and within 0.05°C of an NBS thermometer. T_a was measured at 75 cm because this height is intermediate between the ground where occupants perch and the level at which most intruders fly. The range 75-160 cm includes the heights of ca. 60% of all incoming new arrivals and intruders. The radiation shields were supported by test-tube clamps attached to a 185-cm long, 1.27 cm diameter aluminum rod sunk 20 cm into the ground near the northern boundary of the ground territory.

I also noted the type and extent of cloud cover at various times, including the times when territorial activity starts and ends. Cloud cover was categorized into four groups: clear sky; cirroform (cirrus, cirrostratus); cumuliform (cumulus, altocumulus); and overcast (stratus, stratocumulus). If clouds were broken cumulus or stratocumulus, I recorded times when the sun went in and out. Combined direct and diffuse solar radiation (R_{\odot}) was measured near a butterfly's resting spot with a leveled Li-Cor[®] pyranometer connected to the Micrologger. We moved it from 1-3 times as the occupants switched resting spots as the sun moves. Substrate temperature (T_s) was recorded in the ground territory on 112 days from mid-1988 through 1991 with an 24-AWG thermocouple placed on a patch of bare ground where butterflies often rested. The thermocouple tip was barely covered with a pinch of dry soil or a rubbing of

mud, and the soil surface was described as being either dry or wet. I also used an Everest Interscience, Inc. Model 120 handheld infrared thermometer to take T_s readings of more specific perch sites on both walls and the ground in both territories. Infrared thermometer readings varied no more than 0.3°C from thermocouple readings of the same spots.

To estimate equilibrium body temperature (T_b), another 36-AWG thermocouple was placed in the thorax of a freshly-killed male *V. atalanta* placed in dorsal basking position and tipped up ca. 25° toward the sun. This wire was attached to a 24-AWG lead connected to the Micrologger. I kept the pyranometer and the T_s and T_b probes as closely together as possible (usually within a 60 cm circle) under similar levels of solar radiation, while being sure no probes shaded any others. Both the T_s and T_b probes were calibrated against an NBS thermometer. Wind speed (V_w) is recorded around start time and thereafter at ca. 10-20 min intervals with a Met-One cup anemometer connected to the Micrologger and mounted on the aluminum rod 172 cm above the ground. To estimate conditions affecting incoming arrivals, I took several other wind measurements. The Beaufort Wind Scale was used to estimate wind speed at higher levels (5-10 m) by observing moving flags and tree branches (List, 1971, p. 119). These observations were checked with hourly broadcasts from the National Weather Service Forecast Office, Des Moines, Iowa, ca. 55 km south of the observing site. Prevailing wind direction was monitored by watching a nearby flag, and confirmed from Des Moines Weather Service broadcasts. The 16 compass points were grouped into six direction categories for analysis.

SECTION I. DAILY ACTIVITY SCHEDULE

CHAPTER 1. TERRITORIAL BEHAVIOR OF THE RED ADMIRAL,
Vanessa atalanta (LEPIDOPTERA: NYMPHALIDAE).
 I. THE ROLE OF CLIMATIC FACTORS AND EARLY INTERACTION
 FREQUENCY ON TERRITORIAL START TIME

A paper published in the Journal of Insect Behavior¹

Royce J. Bitzer^{2,3} and Kenneth C. Shaw²

ABSTRACT

We examined the relative importance of climatic factors and population density to territorial start time of *Vanessa atalanta* males. Start time varies with solar altitude and therefore with seasons. We removed seasonal effects by converting start times to corresponding solar altitudes. Start time solar altitude correlates primarily with ambient temperature (T_a) and secondarily with substrate temperature (T_s), regardless of cloud cover. Overcast cloud cover resulted in later not earlier start times as expected from reduced solar radiation (R_\odot) levels. R_\odot may affect start time indirectly by affecting T_s and later start times under overcast skies may be a result of T_s . Start times under solid overcast but not under broken overcast were different than under clear skies, suggesting that *V. atalanta* males can use dim sun or blue patches in broken overcast as a start time cue. Early arrival frequency is correlated with T_a and wind direction,

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²Graduate student and Associate Professor, respectively,
 Department of Zoology and Genetics, Iowa State University.

³Author for correspondence.

but not with start time itself, suggesting that male population density is unimportant compared with climatic factors. We conclude that *V. atalanta* has a climate-dependent start time, but also that maintaining a relatively fixed daily schedule is more important to males than is achieving an optimal body temperature while perching.

INTRODUCTION

Two sets of factors affect when butterflies fly. Climatic factors must permit butterflies to attain body temperatures high enough for vigorous flight (Heinrich, 1981; 1986; Tsuji *et al.*, 1986). Biological factors, such as density of conspecific males (Wickman and Wiklund, 1983; Alcock, 1985; Iwasa and Obara, 1989; Rutowski, 1991) or interspecific competition from other butterflies (Bitzer and Shaw, 1983), may affect whether or when males seek conspecific females while flying (patrolling) and/or while perching (Alcock, 1985; Dennis, 1982; Dennis and Williams, 1987; Rutowski, 1991; Wickman and Wiklund, 1983, Wickman 1985a,b, 1988). Although Scott (1974) considered patrolling and perching as species-specific, these more recent studies have shown that mating strategy in some species changes as both climatic and biological factors vary.

If climatic factors are predictable over the course of the day, then so might be the period when butterflies perch or defend territories. However, if biological factors are also important, butterflies' activity schedules may vary more than one might expect from climatic factors alone. For instance, higher density of conspecific males suggests more scramble competition for territories, which could lead to males perching earlier; alternatively, males might continue to patrol (Wickman and Wiklund, 1983). Energy-wasting heterospecific

interactions between sympatric species could also restrict territorial periods (Bitzer and Shaw, 1983); such temporal exclusion shifts the mainly ambient temperature (T_a)-solar radiation (R_{\odot})-dependent hovering periods of two sympatric tabanid flies (Gaugler and Schutz, 1989). Butterflies may likewise need to avoid periods when predators are active. Layout of a butterfly's habitat (Wickman, 1988) might affect whether or not it has a regular territorial start time at all.

We chose to emphasize climatic factors in this study because their effects were so readily apparent with *V. atalanta*. This contrasts with other species such as *Coenonympha pamphilus* (Wickman, 1985b) in which males perch throughout much of the day, with T_a being but one factor affecting the number of males perching at any one time.

One well-documented relationship is that ambient temperature and solar radiation interact to affect insect body temperature. Vielmetter (1958) described a "change of state" in which the non-territorial nymphalid butterfly, *Argynnis paphia*, switched between continuous flight and stationary basking according to an inverse relationship between T_a and R_{\odot} . When T_a was lower, males flew only when the sun, and therefore solar radiation, was relatively high. On warmer days, males flew longer and did not perch until the sun was lower. Various combinations of T_a and R_{\odot} yielded a critical body temperature (34.2°C) at which butterflies switched behaviors.

These factors may also affect when butterflies establish territories. In our earlier study of *V. atalanta* behavior (Bitzer and Shaw, 1979), we noticed that males started territorial activity later as the days became warmer. Shields

(1967) found that males of four hilltopping species, including *V. atalanta*, perched later on warmer days than on cooler ones.

Seasonal changes in arrival time related to changing solar position should also be evident. In the Northern Hemisphere, lower solar declination during spring and late summer result in the sun reaching particular altitudes earlier in the afternoon than in mid-summer. Brown and Alcock (1991) and Swanson (1979; personal communication) showed that *V. atalanta*'s daily territorial period varied seasonally, the latest occurring toward mid-summer. The nymphalid *Chlosyne californica* (Alcock, 1985) and the lycaenid *Strymon melinus* (Alcock and O'Neill, 1986) showed similar temperature-related and seasonal changes in the times they began territorial behavior. We present a similar model predicting arrival time of *V. atalanta* over the course of the seasons.

Secondary climatic factors which may affect the primary T_a - R_\odot relationship have been relatively neglected. For example, how does cloud cover affect arrival time? R_\odot levels around noon on overcast days are similar to those of late afternoon during sunny days. If *V. atalanta* males simply react to the amount of available solar radiation, they should start territorial behavior much earlier on overcast days. But if they maintain a schedule similar to that on sunny days, this suggests an endogenous circadian rhythm. Do *V. atalanta* males start territorial behavior at the same or different times on days of solid vs. broken overcast? If they arrive on days with broken overcast at times similar to those for sunny days, but arrive at different times on solid-overcast days with similar R_\odot , they may be using sky patches or dim sun as visual cues to start territorial behavior.

Substrate temperature may also affect when *V. atalanta* and other butterflies start and maintain territorial activity. Wickman (1988) suggested that *Lasiommata megera* males often had to choose between an optimal perch temperature or an optimal T_a for flight. Shreeve (1984) found that patrol duration in *Pararge aegeria* depended upon T_a , whereas perching duration depended upon R_{\odot} and substrate temperature (T_s). Alcock (1985) suggested that *V. atalanta* males perching on the ground may maintain optimal body temperatures at a lower metabolic cost than when patrolling. If *V. atalanta* males are heated significantly by the substrate upon which they perch, T_s at a particular territory could affect whether or not they choose to stay there or fly off in search of a warmer site. Reconnaissance flights and brief, temporary perchings of butterflies before territorial activity actually begins suggest that butterflies assess conditions at prospective territorial sites. Since T_s is lower on cloudier days, a better test of this hypothesis would be to compare arrival times on sunny days when the T_s are very different.

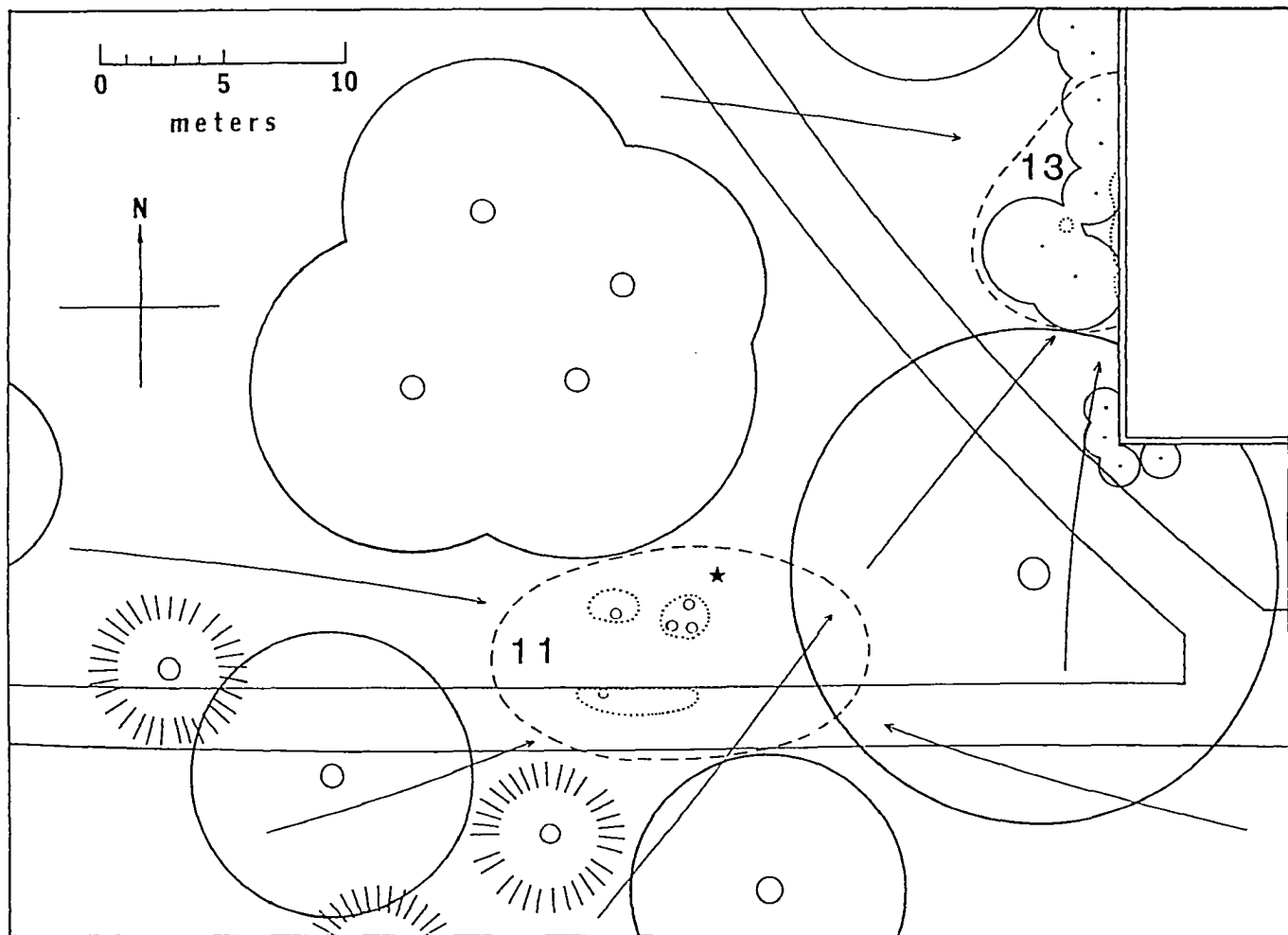
We present evidence that a male's daily "decision" to start territorial behavior is more complex than the simple "change of state" response which Vielmetter (1958) described. We identify correlations of several climatic variables with territorial start time and determine their relative importance. We also establish models to which arrival time of other populations or species might be compared. These findings will provide a basis for future experimental work on arrival time.

MATERIALS AND METHODS

Butterflies were observed on the Iowa State University campus between April and September from 1987-1991. We recorded a total of 224 start times, defined as the time when a *V. atalanta* male first landed and then stayed in a territory, patrolling it at least once and/or interacting with at least one intruder. Brief perchings or circlings of butterflies were not counted as start times, but were also recorded and correlated with climatic factors. To minimize possible start time variation due to site-dependent factors, we observed only two optimal [most frequently occupied (Bitzer and Shaw, 1979)] territories and distinguished them in our analyses. Territory 11 was located on the ground in a clearing that was open to the west and bounded on the other three sides by trees (Fig. 1). The other site, Territory 13, was located along a partially sunlit wall in another clearing flanked by trees (Fig. 1). Sunlight fell in both areas most strongly before 1600h CST, then became increasingly patchier, and was gone by 1910-1930h. Start time was usually recorded in Territory 11 (166 of 224 obs.) unless butterflies perched only in Territory 13. On 32 days, we recorded start times in both territories.

To estimate population density around start time, we recorded early arrival frequency. With 164 start times, we recorded when the first two intruders arrived at occupied territories. If the initial occupant perched and patrolled but left before an intruder arrived, we counted the subsequent arrival as the "first intruder." Based on marking studies (Bitzer and Shaw, 1979; unpublished data) and our ability to recognize unmarked butterflies, we estimated that no more than 5% of the 328 first and second intruders were repeat visitors during the following two weeks. Intervals between start time and first intruder, and

Figure 1. Two territories observed on the ISU campus, 1987-1991. Dashed lines: typical territorial boundaries. Arrows: routes along which butterflies frequently entered territories. Solid lines: sidewalks and buildings. Small circles with central dots: shrubs near building. Large circles with rings near centers: canopy trees and trunks. Sunbursts: columnar spruce trees. Numbers: territory designations. Dotted ellipses: territorial resting spots. O: locations of pyranometer, T_s , and T_b probes. ★: Location of pole with anemometer and thermocouples.



between first and second intruders were averaged to yield a single value of early arrival frequency.

All times were recorded to the nearest second (Central Standard Time) with a digital quartz clock/stopwatch set by time signals from the National Bureau of Standards (NBS) radio station WWV, and were converted to four-place decimal equivalents. Solar altitude corresponding to each start time was calculated as in Campbell (1977, p. 53). Latitude ($42^{\circ}01'38''$ N) and longitude ($93^{\circ}38'42''$ W) of the territorial sites were taken from a USGS topographical map. Solar declination (δ , angular distance of the sun north or south of the equator) and ephemeris time of solar noon were taken from the *Astronomical Almanac* (1987-1991). Time of solar noon was corrected for longitude. We then subtracted 12h from this corrected value to obtain the solar noon variation (ϵ), the difference between CST and local solar transit time.

Ambient temperature (T_a) was recorded from 1987 to 1991 with a shaded, aluminum-encased thermometer suspended 75 cm above the ground, a height intermediate between those of perching and most flying butterflies. T_a was recorded at 5-10 min intervals before start time, within 1 min afterward, and at 10-20 min intervals thereafter. A 10-20 min interval was the shortest period during which the thermometer noticeably dropped (0.1°C), except on days with broken cloud cover. This thermometer was calibrated against an NBS standard thermometer.

During 1989-1991, T_a was also recorded at altitudes of 13, 75, and 160 cm with three white-tube-shielded 24-AWG copper-constantan thermocouples attached to a Campbell Scientific 21X Micrologger[®]. All thermocouple probes used read within 0.05°C of each other in water (at both 0° and 45°C), and within

0.05°C of the NBS thermometer. The range 75-160 cm included the heights of ca. 60% of all incoming new arrivals and intruders. Radiation shields were clamped to a 185-cm-tall aluminum rod placed near the northern boundary of Territory 11 (Fig. 1).

We also noted type and extent of cloud cover around start time. Cloud cover was classified into five groups: clear sky; cirroform (cirrus, cirrostratus); cumuliform (cumulus, altocumulus); solid overcast (stratiform), and broken overcast (stratus or stratocumulus with sun dimly visible and/or with patches of blue over more than 2% of the sky). If clouds were cumulus or broken stratocumulus, we recorded times when the sun went in and out. Combined direct and diffuse solar radiation (R_{\odot}) were measured near a butterfly's resting spot during 1989-1991 with a leveled Li-Cor[®] pyranometer connected to the Micrologger[®]. We moved it from 1-3 times as butterflies switched resting spots as the sun moved.

Substrate temperature (T_s) was recorded in Territory 11 on 112 days from mid-1988 through 1991 with a 24-AWG thermocouple placed on a patch of bare ground where butterflies often rested. The thermocouple was barely covered with a pinch of dry soil or a rubbing of mud, and the soil surface was described as being either 'dry' or 'moist.' We used an Omega HH-73 microcomputer thermometer from 14 June-2 September 1988, and the Micrologger[®] thereafter. We also used an Everest Interscience, Inc. Model 120 handheld infrared thermometer during 1991 to read T_s of perch sites in both territories. These readings varied no more than 0.3°C from thermocouple readings of the same spots. Emissivity of soil and stone was assumed to be 0.95; that of vegetation,

0.98, in accord with standard practice (see Monteith and Unsworth, 1990, pp. 81-85).

To estimate equilibrium body temperature (T_b), a 36-AWG thermocouple was inserted into the thorax of a freshly-killed male *V. atalanta* placed in dorsal basking position and tipped up ca. 25° toward the sun (see Polcyn and Chappell, 1986). The thermocouple was attached to a 24-AWG lead connected to the Micrologger®. We kept the pyranometer and the T_s and T_a probes within a 60-cm circle under similar levels of solar radiation, with no probes shading any others.

Wind speed (V_w) was recorded around start time and thereafter at ca. 10-20 m intervals with a cup-type anemometer mounted 172 cm above the ground. This was replaced in 1989 with a Met-One® cup anemometer attached to the Micrologger®. Prevailing wind direction was monitored by watching a nearby flag, and was confirmed from readings broadcast by the National Weather Service Forecast Office, Des Moines, Iowa, ca. 55 km south of the observing site. The 16 compass points were grouped into six direction categories for analysis.

Multiple regression and analysis of covariance (ANCOVA) were used as statistical models after simple correlations were used to check for possible confounded variables. Adjusted means with t-tests were used to compare classes within categorical variables in the ANCOVA's.

RESULTS

Climatic Factors

Start Time Varies with Ambient Temperature and Time of Year

Start time was later when T_a was higher (Fig. 2, $R^2=0.56$, $F=268.08$, $P<0.0001$, $n=214$). Predicted start times increased linearly by 8.98 min for each additional 1°C of T_a .

Butterflies began perching 20-50 min earlier at the same T_a in early May and in August through September than they did from mid-May through July (Fig. 2). Seasonal changes in both solar declination (δ) and time of solar noon (ϵ) correlated with start time (multiple regression, Table I. Start times for any particular T_a were earlier when δ was lower, and also followed seasonal variations in ϵ . Accounting for both δ and ϵ explained an additional 12% of the residual variability in the first model ($R^2=0.68$, $F=159.12$, $P<0.0001$, $n=224$).

Regressing the solar altitudes corresponding to each start time (=start time solar altitude or STSA) against T_a (Fig. 3) combined start time, δ , and ϵ into a single factor, giving us a model ($R^2=0.61$, $F=335.02$, $P<0.0001$, $n=214$) analogous to Vielmetter's (1958) analysis. The sun averaged $1^\circ.60$ lower (ca. 8.98 min later) at start time for each increase of 1°C . Start time was even more predictable for sunny days ($R^2=0.67$, $F=190.94$, $P<0.0001$, $n=97$). Like *A. paphia* (Vielmetter, 1958), *V. atalanta* males on sunny days start perching based on an inverse relationship between T_a and solar altitude, the latter determining the amount of solar radiation. Solar radiation (R_\odot) on clear afternoons decreases linearly with solar altitude. Plotting the solar altitude at start time against T_a thus yields a plot analogous to those of Vielmetter (1958). Plotting arrival time of territorial butterflies as a solar altitude value allows one

Figure 2. Relationship of ambient temperature (T_a) and solar declination (δ) to start time (hours CST).

Sky conditions: + : Clear sky; O: Cirroform cloudiness; V: Cumuliform cloudiness; ◆: Broken overcast; ▲ : Solid overcast. — : Regression line for all 224 observations (Start time = $13\text{h}.03 + 0.15 T_a$). - · - · - · - : Predicted start time line for 21 June ($\delta = +23^\circ.4433$). - - - - - : Predicted start time line for 21 April/August ($\delta = +12^\circ$). To simplify the graph, time of solar noon was set at 12h 16 min 51s (12h.2807), near the mean value for all data; thus $\epsilon = 16 \text{ min } 51\text{s} (0\text{h}.2807)$. Start time = $11\text{h}.35 + 0.13 T_a + 0.060 \delta + 3.26 \epsilon$.

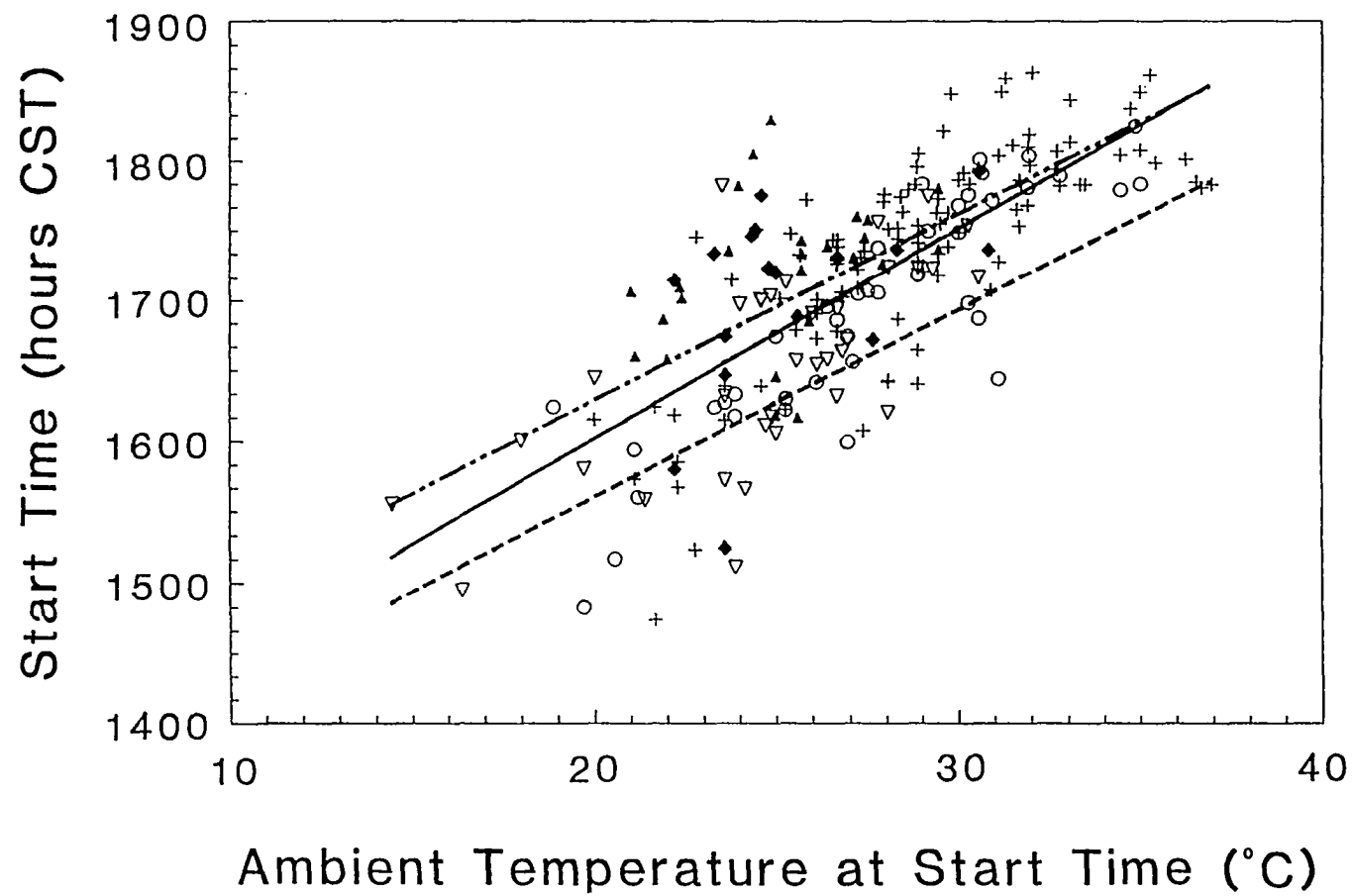


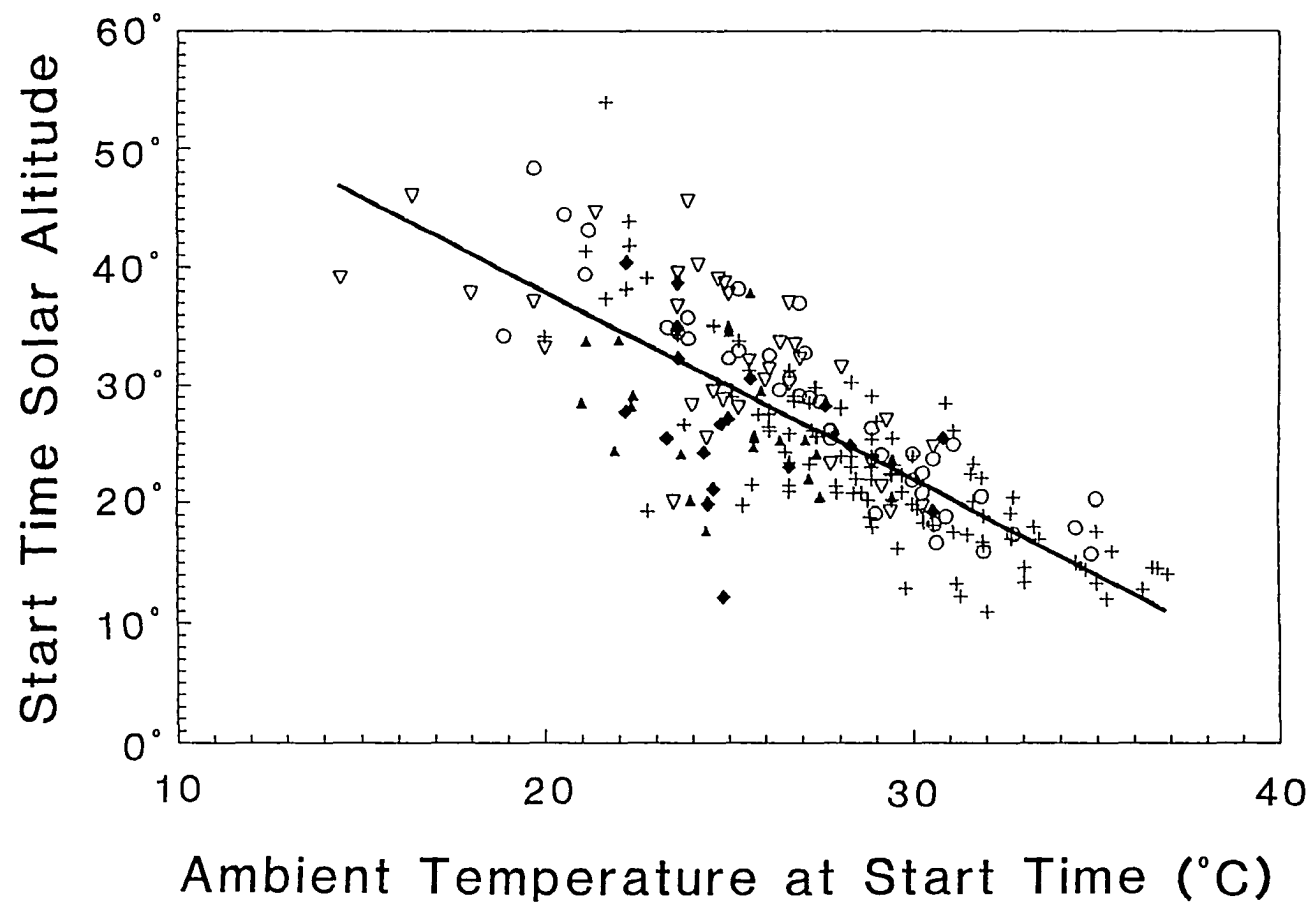
Table I. The Effect of Ambient Temperature, Solar Declination, and Solar Noon Variation^a Upon Start Time.^b

Source	df	SS	<i>F</i>	<i>P</i>
Ambient Temp. (T_a)	1	53.01	262.01	<0.0001
Declination (δ)	1	9.70	47.96	<0.0001
Solar noon variation (ϵ)	1	6.64	32.81	<0.0001

^aStandard Time of solar transit - 12 h.

^bStart time = 11h.35 + 0.13 T_a + 0.060 δ + 3.26 ϵ . $R^2 = 0.68$, $F = 159.12$,
 $P < 0.0001$, $n = 224$, 3 treatment df.

Figure 3. Relationship of ambient temperature (T_a) to start time (expressed as the corresponding solar altitude). Sky conditions are indicated as in Fig. 2. $STSA = 69^\circ.94 - 1.60 T_a$.



to compare activity schedules of both different populations and different species located in various latitudes.

Correlation of Ambient Temperature, Cloud Cover, Wind Velocity, Wind Direction, Territory Site, and Year with STSA

An ANCOVA model including all variables showed that T_a , cloud cover, and year all correlated with STSA, and therefore with start time (Table II, ANCOVA with significant variables). T_a accounts for most of the attributed variance and is by far the most important correlate of STSA. Comparing the four types of cloud cover with clear skies showed that butterflies started later on solid overcast afternoons than on clear ones (Table II). Earlier start times under cirroform and cumuliform cloudiness approach significance (Table II) or are insignificant, depending upon which of the above variables are in the model.

The start time- T_a relationship varied from year to year, averaging the earliest in 1989 and 1990, intermediately in 1987 and 1988, and latest in 1991. 1991 start times were consistently later than those of the preceding four years (range of t : 3.28-8.06, $P=0.0012$ to <0.0001). Wind speed, wind direction, and territory site did not seem to affect start time.

Relationship between Ambient Temperature and Solar Radiation at Start Time

Plotting R_{\odot} against T_a at start time emphasizes the marked difference in energy available from solar radiation on sunny vs. cloudy days (Fig. 4). An ANCOVA model for the five sky conditions ($R^2=0.68$, $F=22.75$, $n=60$, $P<0.0001$) indicated a highly significant difference between overcast and clear days ($t=-9.29$, $P<0.0001$, $n=60$).

Table II. The Effect of Ambient Temperature, Year, and Cloud Cover upon Start Time (Expressed as Solar Altitude^a).

Source	df	SS	<i>F</i>	<i>P</i>
Ambient temp. (T_a)	1	5276.50	299.02	<0.0001
Year	4	1211.17	17.16	<0.0001
Cloud cover	4	477.91	6.77	<0.0001

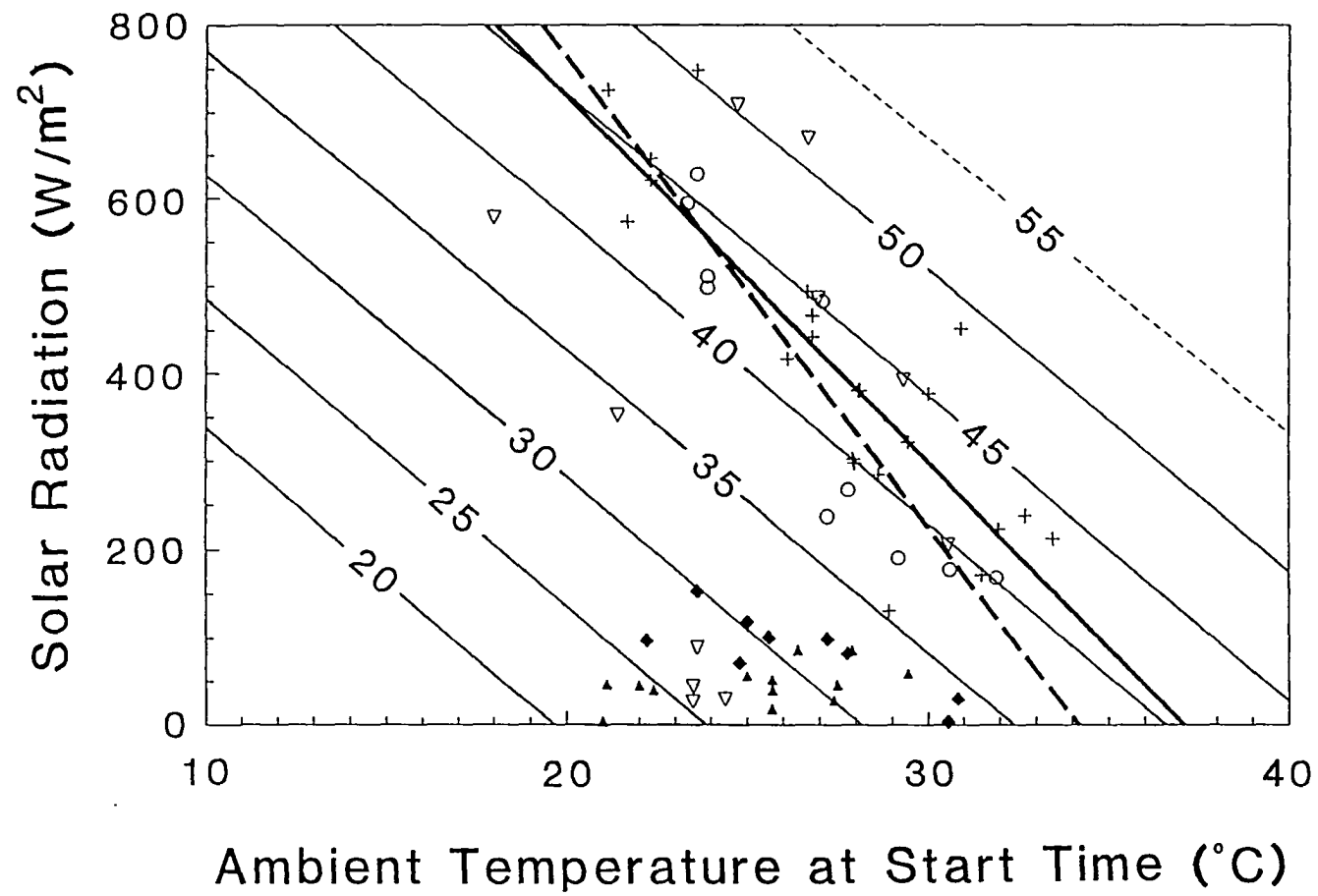
Year	Adjusted mean STSA	Year difference	Different from 1991? <i>t</i>	<i>P</i>
1987	24°.61	3°.08	3.17	0.0018
1988	26°.06	4°.53	5.01	<0.0001
1989	28°.94	7°.41	7.79	<0.0001
1990	27°.54	6°.01	5.75	<0.0001
1991	21°.53	0	-	-

Cloud cover	Adjusted mean STSA	Cloud cover difference	Different from clear? <i>t</i>	<i>P</i>
Solid overcast	22°.33	-3°.69	-3.46	0.0007
Broken overcast	24°.99	-1°.02	-0.86	0.3881
Cumuliform	27°.79	1°.77	1.97	0.0505
Cirroform	27°.58	1°.56	1.93	0.0546
Clear	26°.01	0	-	-

^aSTSA = $61°.96 - 1.47 T_a + \text{year difference} + \text{cloud cover difference}$. $R^2 = 0.75$, $F = 66.89$, $P < 0.0001$, $n = 214$, 9 treatment df.

Figure 4. Correlation of ambient temperature (T_a) and solar radiation (R_{\odot}) at start time on 62 days. Sky conditions are indicated as in Fig. 2. — : Regression for clear-sky observations.

- - - - : Regression for perching threshold of *Argynnis paphia* (Vielmetter, 1958). Sloping contours are isotherms of equilibrium body temperature (T_b) of freshly-killed *V. atalanta* males in dorsal basking position, measured at 1-min intervals 5 min before-5 min after start time on 35 of these days (n=359). After T_a and R_{\odot} are located on the axes, the predicted T_b for these values is read from the diagonal isotherm contours at the point where perpendiculars to the axes intersect. *V. atalanta*: $R_{\odot} = 1557.46 \text{ W/m}^2 - 41.94 T_a$. $T_b = 0.034 R_{\odot} + 1.19 T_a - 3.42^\circ$. *A. paphia*: $R_{\odot} = 1838.59 \text{ W/m}^2 - 53.76 T_a$.



The T_a - R_{\odot} regression line for sunny days ($R^2=0.74$, $F=54.15$, $P<0.0001$, $n=22$) is similar to that for the butterfly *A. paphia* (Vielmetter, 1958) and lies between the 40° and 45° body temperature (T_b) isotherms (Fig. 4). The x-intercept of the regression line, 37.1°C with $R_{\odot}=0$, estimates preferred T_b .

V. atalanta males tended to perch on non-overcast days with wings closed ($n_1=37$) when T_a was higher and wings open ($n_2=29$) when T_a was lower ($t=2.68$, $P=0.0093$, $n=66$).

Substrate Temperature and Start Time

Simple correlations of T_s , T_a , cloud cover, and R_{\odot} showed that T_a and T_s were not confounded on clear and cirroform-clouded days (partial correlations, $r=-0.13$, $P=0.35$; $r=-0.40$, $P=0.10$, respectively). They were positively correlated for all sky conditions ($r=0.39$, $P<0.0001$, $n=112$) only because T_a and T_s were similar on overcast and cumulus days. We thus included T_s as a secondary variable in STSA vs. T_a models.

Cloud cover is highly correlated with both R_{\odot} ($r=0.62$, $P<0.0001$, $n=61$) and T_a ($r=0.32$, $P=0.0006$, $n=112$). Since T_s is also highly correlated with cloud cover ($r=0.51$, $P<0.0001$, $n=112$), cloud cover is likely the main factor affecting T_s .

In an ANCOVA model of start time solar altitude vs. T_a , T_s , year, and cloud cover ($n=112$, mid-1988 through 1991), T_s was highly significant, second to T_a (Table III). Differences between cloud cover disappeared, and only in 1991 was STSA significantly different from the other three years ($t=3.81$ -5.36, $P=0.0002$ to <0.0001).

Table III. The Effect of Ambient and Substrate Temperatures, Year, and Cloud Cover upon Start Time (Expressed as Solar Altitude^a).

Source	df	SS	<i>F</i>	<i>P</i>
Ambient temp. (T_a)	1	3687.41	218.34	<0.0001
Substrate temp. (T_s)	1	305.05	18.06	<0.0001
Year	3	622.92	12.29	<0.0001
Cloud cover	4	52.49	0.78	0.5427

Year	Adjusted mean STSA	Year difference	Different from 1991? <i>t</i>	<i>P</i>
1988	28°.17	4°.96	4.22	<0.0001
1989	28°.86	5°.65	5.30	<0.0001
1990	28°.44	5°.24	3.82	0.0002
1991	23°.21	0	-	-

^aSTSA = $56°.04 - 1.72 T_a + 0.40 T_s + \text{year difference}$. $R^2 = 0.80$, $F = 44.19$,
 $P < 0.0001$, $n = 112$, 9 treatment df.

In a two-variable model ($R^2=0.70$, $F=124.99$, $P<0.0001$, $n=112$), start times at any particular T_a tended to be early when T_s was high and late when T_s was low (Fig. 5). Start time solar altitude was $1^\circ.86$ lower (ca. 10.4 min later) for each 1°C increase in T_a ($F=249.98$, $P<0.0001$), but $0^\circ.52$ higher (ca. 2.9 min earlier) for each 1°C increase in T_s ($F=37.77$, $P<0.0001$).

Since T_s was correlated with STSA on clear days ($F=7.81$, $P=0.0002$), start time varies with T_s independently of the effects of cloud cover. In 1991, for instance, T_s was considerably lower on sunny days than during previous years; start times were also considerably later. However, we must examine the possibility that generally cooler conditions which reduced T_s in 1991 may have caused later start times by reducing population density. Since no differences in early arrival frequency were evident between years, and T_s is not correlated with arrival frequency, a direct effect of T_s remains a possibility.

Relative Importance of Ambient Temperature, Surface Temperature, and Solar Declination

We now present our model again as a function of time rather than altitude. In a multiple regression of start time vs. T_a , solar declination, T_s , and time of solar noon (Table IV), T_a was the strongest factor, followed by δ , T_s , and ϵ . As in Fig. 2, start time for any given T_a becomes earlier when δ is lower; it also becomes later when T_s is lower and ϵ is later.

Climatic Correlates of Behavior Before Start Time

Some pre-perching investigation of sites was correlated with T_a but not with T_s . As compared with days on which we observed no pre-perching behavior (mean $T_a=27.01^\circ\text{C}$), brief perchings ($t=-2.90$, $P=0.0042$) were associated with

Figure 5. Relationship of ambient (T_a) and substrate (T_s) temperatures to start time (expressed as STSA).
..... : $T_s = 25^\circ\text{C}$. ————— : $T_s = 35^\circ\text{C}$. - - - - - : $T_s = 40^\circ\text{C}$. Sky conditions
are indicated as in Fig. 2. $\text{STSA} = 60^\circ.05 - 1.86 T_a + 0.52 T_s$.

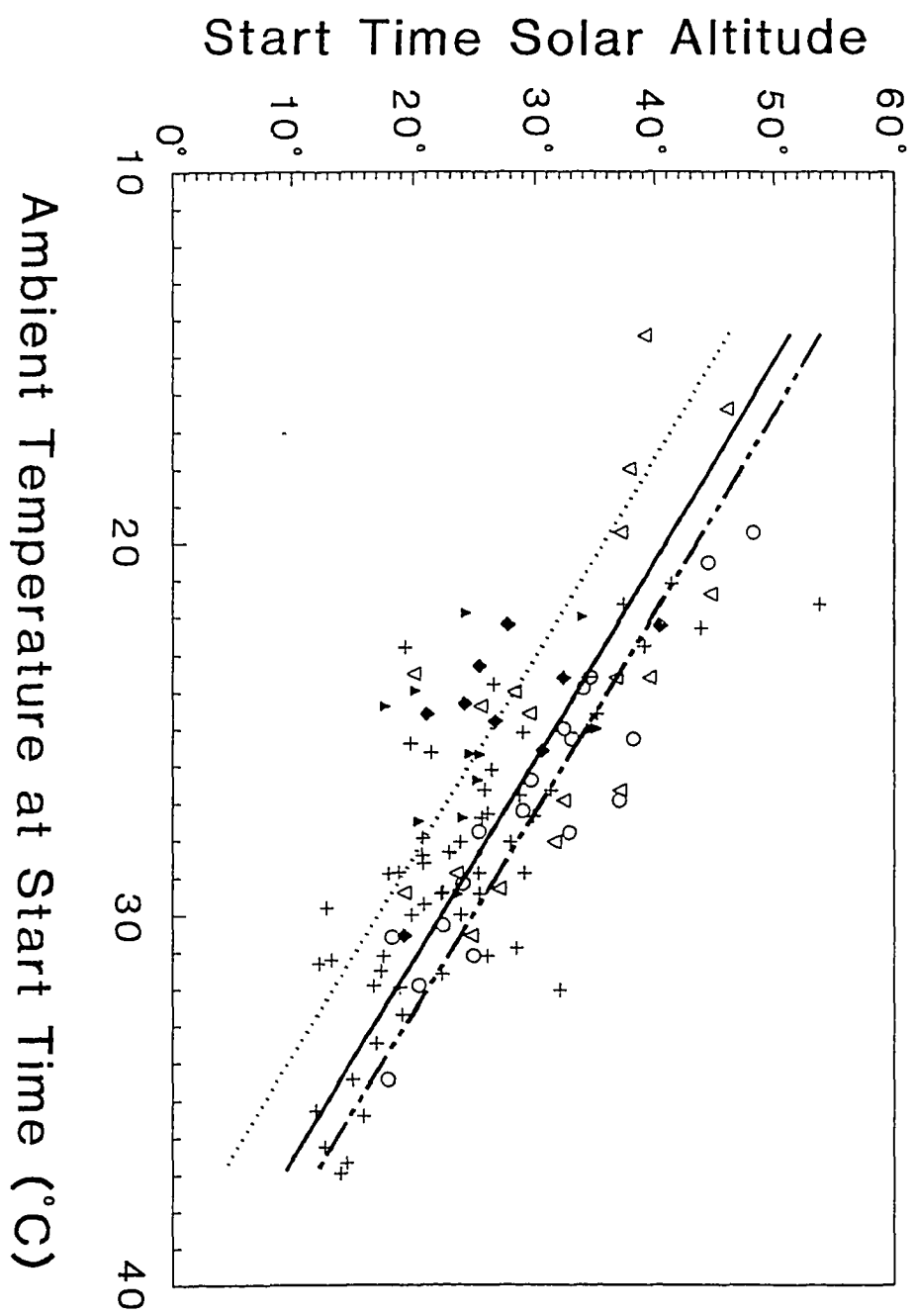


Table IV. Effects of Ambient Temperature, Solar Declination, Substrate Temperature, and Solar Noon Variation^a upon Start Time.^b

Source	df	SS	<i>F</i>	<i>P</i>
Ambient temp. (T_a)	1	29.74	170.54	<0.0001
Declination (δ)	1	9.32	53.46	<0.0001
Substrate temp. (T_s)	1	7.44	42.66	<0.0001
Solar noon variation (ϵ)	1	3.18	18.24	<0.0001

^aStandard Time of solar transit - 12 h.

^bStart time = $11\text{h}.98 + 0.15 T_a - 0.048 T_s + 0.076 \delta + 3.59 \epsilon$. $R^2 = 0.77$,
 $F = 89.55$, $p < 0.0001$, $n = 112$, 4 treatment df.

lower mean T_a (24.67°C), whereas butterflies flew beelines through territories when mean T_a was higher (28.69°C, $t=2.13$, $P=0.0347$; ANOVA, $R^2=0.12$, $F=6.11$, $P<0.0001$, $n=188$). Circling reconnaissance flights were not associated with either low T_a or low T_s , nor were brief perching or beelining associated with T_s in any way (ANOVA, $R^2=0.0082$, $F=0.38$, $P=0.82$).

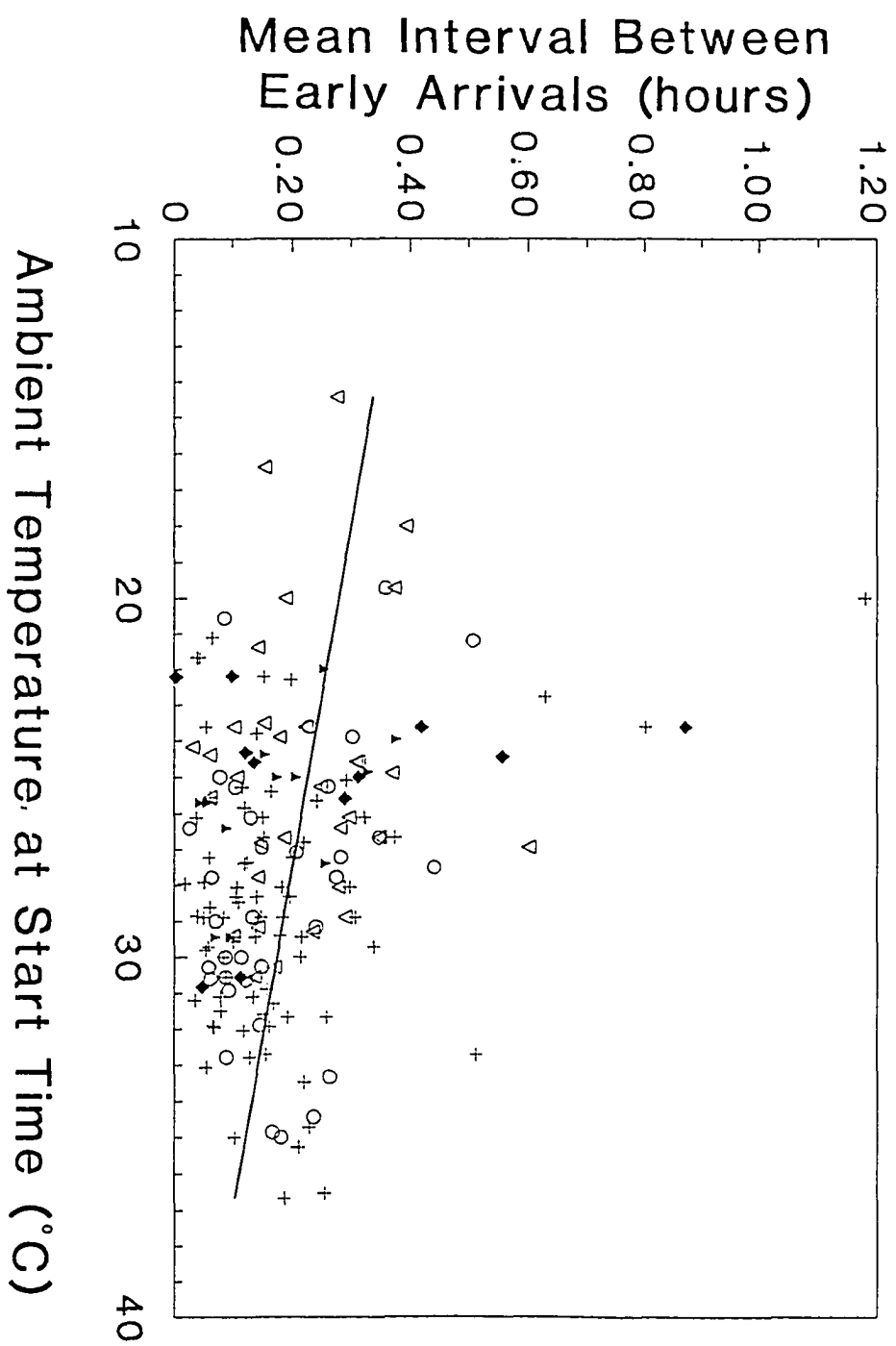
Population Density Factors

Start Time and Arrival Frequency

Start time does not vary with the number or density of flying butterflies active just after start time. Very early or very late start times on some days were not correlated with shorter or longer intervals between the first three arrivals (regression of absolute values of residuals, $F=0.02$, $P=0.8875$, $n=164$). The subsequent activity level was as intense as on days when butterflies started on time. Also, *V. atalanta* males did not start earlier when the initial arrival frequency was higher and later when it was lower ($F=0.02$, $P=0.8962$, $n=164$).

Early arrival frequency does increase on warmer days (Fig. 6; $F=11.27$, $P=0.0010$, $n=164$). Arrival frequency also varies by wind direction ($F=3.36$, $P=0.0066$). It was highest with NE through SE winds, with both territories being sheltered by a building (Fig. 1), and lowest with SSE through W winds, when the site was most exposed. Early arrival frequency did not vary with year ($F=1.35$, $P=0.2542$), cloud cover ($F=0.24$, $P=0.9134$), or T_s ($F=0.95$, $P=0.3330$, $n=93$). Mean temporal spacing of early arrivals varies by the formula, $0h.49 - 0.0105 T_a$ (ANCOVA, $R^2=0.16$, $F=4.94$, $P<0.0001$, $n=164$).

Figure 6. Relationship of ambient temperature (T_a) to mean temporal spacing of the first three arrivals.
Sky conditions are indicated as in Fig. 2. Mean arrival interval = $0.49 \text{ h} - 0.011 T_a$.



DISCUSSION

To fly, locate mates, defend territories, etc., butterflies must obtain heat from the environment. The sun heats the air through which they fly, warms the substrate on which they perch, and warms their bodies directly. As T_a increases, start time gets later, presumably because less heat is needed from other sources. Later in the day, the sun's altitude is lower and less radiational heat is available. Start times are earlier in spring and late summer than in mid summer because the sun then reaches a particular altitude earlier in the afternoon.

Excluding seasonal effects, *V. atalanta* territorial start time is correlated primarily with T_a and secondarily with T_s . R_{\odot} seems to affect start time indirectly by affecting T_s . Cloud cover reduces R_{\odot} and therefore T_s . When T_s is cooler than average, *V. atalanta* males perch late, even on sunny days with high R_{\odot} levels.

Interrelationship of Ambient Temperature, Solar Radiation, and Substrate Temperature Effects

On sunny days, falling R_{\odot} and T_a may induce *V. atalanta* males, like non-territorial *A. paphia* (Vielmetter 1958), to switch from flying to perching to maintain their preferred body temperature. Similar T_a - R_{\odot} relationships affect activity schedules of many insects, including the hovering period of tabanid flies (Gaugler and Schutz, 1989). Judging from the x-intercepts in Fig. 4, *V. atalanta* seems to prefer higher T_b than does *A. paphia*. This difference may be due to adaptation to local conditions or to greater energy requirements for *V. atalanta* because territorial males need to mate, patrol, and chase intruders. Just after

they perch, live *V. atalanta* males have a greater need to bask dorsally on cooler days.

However, since *V. atalanta* males maintain a similar T_a -dependent timetable on overcast as well as sunny days, start time of perching cannot be solely a response to radiational heat as Vielmetter (1958) suggested for *A. paphia*. Equilibrium T_b values for recently-killed *V. atalanta* males are considerably lower at territorial start times on cloudy days than at equivalent air temperatures on sunny days (Fig. 4). Even so, territoriality can be as intense on cloudy as on sunny days. *V. atalanta* males must therefore generate metabolic heat to maintain T_b levels high enough for intense patrolling and interacting. The actual T_b of live butterflies on overcast days is 8-12°C above the equilibrium value (unpublished data).

V. atalanta males vibrate their wings when perched in the shade on cool days; Krogh and Zeuthen (1941) found that *V. atalanta* can raise its thoracic temperature from 20 up to 35.5°C in this way. They also fly vigorously on cloudy days above 23°C, with body temperatures at or above the 32°C level (unpublished data) which Heinrich (1986) found necessary for *V. atalanta* to fly vigorously.

These findings suggest that *V. atalanta* males perch primarily to await females and secondarily to maintain optimal body temperatures. This behavior contrasts with that of *Pararge aegeria*, which perches on sunny but not on overcast days (Davies, 1978; Dennis, 1982). If initiation of perching depended solely upon response to radiational heat, butterflies should start territorial behavior around noon on overcast days, when R_{\odot} levels are similar to those of late afternoon on sunny days, rather than ca. 0.5-1 h later on overcast days. The

data for cirroform cloudiness do suggest (approaching significance) that *V. atalanta* males under thin cirrus-veiled skies compensate for reduced R_{\odot} by perching slightly earlier in the afternoon.

Later start times on overcast days may be related to the role of T_s . T_s is as important as T_a to *V. atalanta* males in maintaining T_b . T_b increases ca. 1°C for each 2°C rise in T_s under constant T_a and R_{\odot} (unpublished data).

Butterflies either gain heat from ground radiation or reduce the loss of heat gained from the air and solar radiation. Most heat exchange between the butterfly and the ground probably occurs via air trapped between the ground and the spread wings of the basking butterfly (see Clench, 1966).

A surprising finding was that territorial start time was more strongly correlated with T_s than with R_{\odot} . Solar radiation may be relatively unimportant to *V. atalanta* because *V. atalanta* perch sites are often patchily sunlit and males frequently rest in partial sun or shade later in the territorial period. They may thus prefer a perch warmed earlier in the day as much as they do a sunny perch. A wide range of T_s occurs, even on sunny days, because T_s depends partly upon subsurface heat storage, and thus upon weather hours to weeks before as well as from momentary conditions.

Why are start times earlier when T_s is higher? If there is a real cause-and-effect relationship, one expects that a flying male would not take note of T_s until declining T_a induces him to seek a territory. Once he perches in a warm area, he is likely to stay there. If the ground is cool, however, he may decamp and keep flying longer and look for a warmer spot as long as the presumed benefits of searching exceed the costs of not perching. Failure to find any warm substrates at all could explain cloudy-day start times which are typically later

than if start time depended only upon availability of heat energy. Departure times are also earlier on overcast days, resulting in shorter territorial periods (Bitzer and Shaw, in preparation.), which reduce the demand for metabolically-derived heat energy.

T_s -associated start time variation on sunny days most strongly supported this hypothesis. Since early arrival frequency, and thus population density, is not correlated with either year or T_s , there is no indication that cooler weather conditions which reduced T_s in 1991 caused lower population densities, which might have led to later start times by reducing male scramble competition for territories. A direct effect of T_s upon start time thus remains a possibility.

One problem with this hypothesis is that *V. atalanta* males tend to perch briefly and leave territories when T_a , rather than T_s , is low, and reconnaissance flights are not correlated with temperature at all. Another problem is the great difference between arrival times under broken vs. solid overcast, when R_{\odot} levels are similarly low. An alternative possibility on overcast days is that a yet-unknown interspecific competitor could prevent *V. atalanta* males from perching very early on such days. But this hypothesis would not explain why they perch *late*. Further work is needed before we can say with certainty that T_s is the main source of secondary start time variation.

Our finding that *V. atalanta* males set up territories later on days with solid overcast, but not on days with broken overcast, as compared with sunny days, suggests that they may directly sight the sun's altitude as a cue to perch when direct solar radiation is weak or absent. Their ability to maintain a regular schedule under solid overcast suggests a circadian rhythm modulated by T_a and possibly other climatic factors.

The Effects of Wind Around Start Time

The lack of a wind velocity effect upon start time was also unexpected. Since *V. atalanta* males often flew steadily toward territories from considerable distances just before perching, they should cool significantly more in flight on windy days and should thus perch earlier. Lack of a V_w effect may occur partly because some occupants rest sheltered from wind in the branches of nearby trees just before start time. Vielmetter (1958) found no significant wind effect upon the T_a-R_{\odot} relationship for perching *A. paphia* due to low variability in V_w from day to day and a lack of calm days for comparison. However, we found that V_w varied from calm to gusts of 20 m/s, with 1-min averages varying from 0-6 m/s, indicating a broad range of wind conditions.

Variations in early arrival frequency with wind direction suggest local winds from some directions more than others may discourage incoming intruders, even though start time itself does not depend upon wind direction.

Once *V. atalanta* males have perched, they are well-protected from wind. V_w is generally much lower near the ground (Campbell, 1977, pp. 37-40); the effect of V_w (measured at 1.72 m where intruders fly) on T_s was small to insignificant (unpublished data). We have found that except during calm periods, freshly-killed perched *Vanessa cardui* probes stay warmer than those suspended at flight level throughout the similar territorial period of this species (unpublished data). Alcock (1985) suggests that male *Vanessa* butterflies perching on the ground may maintain optimal body temperatures at a lower metabolic cost than by patrolling.

Interpopulation Variation of Start Time

V. atalanta males in some other parts of the United States do not react to T_a and R_{\odot} in the same way as does the population in Ames, Iowa. Although the slope of Shields' (1967) start time line for *V. atalanta* (8.74 min/°C) was similar to ours, his observations in southern California were nearly 10° further south in latitude. At 32°N, solar altitude decreases more rapidly during the afternoon. Thus, Shields' data suggest that STSA decreases more steeply with increasing temperature in California *V. atalanta* populations. In a north-central Florida population, on the other hand, STSA decreases by only 0°.80/°C, half the rate (1°.60/°C) as in Iowa *V. atalanta* (Swanson and Bitzer, in preparation.). Here in Iowa, seasonal changes in solar declination caused much less variability (14-19% of model variability) in start time than Brown and Alcock (1991) found in Arizona *V. atalanta* (50%). This difference is likely due to the relatively small variation in solar declination during our shorter activity season. Activity schedules in other areas could also be more density-dependent, resulting in greater variance of start times around the climate space boundary. This may be true in Florida (Swanson and Bitzer, in preparation).

One should therefore be cautious when comparing start time from different locations. Even in the same area, the STSA vs. T_a relationship may vary from year to year, possibly due to such diverse factors as yearly T_s or population density variations, acclimation, or immigration from genetically distinct populations which one might not expect to find in a butterfly as cosmopolitan and migratory (Larsen, 1993) as *V. atalanta*.

Habitat Variation and Intra- and Interspecific Differences in Daily Schedule and Territorial Behavior

Whether or not a butterfly starts territorial behavior at a predictable time may also depend upon its habitat, as will the relative importance of T_a , T_s , R_\odot , and V_w . Moderately high T_b on sunny days and the small V_w and great R_\odot effects upon T_s indicate that *V. atalanta* perch sites are thermally optimal at start time on sunny days as well as usually protected from rapid microclimate fluctuations.

Lasiommata megera (Satyridae) males perch on rocky, sparsely-vegetated hilltops most of the day and move around or up or down the hill as the sun's azimuth, T_a , T_s , V_w , etc. change (Wickman, 1988). *L. megera* males can choose sites of various slopes and sun exposures and thus need not be tied to a particular climatic schedule. T_s and near-ground T_a are often excessive at these sites, as is V_w , which affects both these factors much more strongly than upon flat ground (Wickman, 1988). *V. atalanta*, in contrast, uses patchily-lit but well-sheltered spots on flatter ground and so must wait for the sun to move to a particular altitude. Overly high T_s is rare in *V. atalanta* territories; males can avoid sunspots anyway by moving to shade, as does the nymphalid butterfly *Asterocampa leilia* (Rutowski *et al.*, 1991). Only on days when T_a was above 33°C at start time did *V. atalanta* males ever reject a sunlit territory and go to a shady one. *A. leilia* in open, arid sites in central Arizona escape hot ground by moving onto vegetation (Rutowski *et al.*, 1991). Although *V. atalanta* never escaped high T_s this way, we have seen them re-perch on sunlit branches 4 m up soon after arrival on 5 sunny days when T_s was unusually low (< 30°C).

Butterflies living beneath forest canopy (Davies, 1978; Shreeve, 1984) often fly through shade, and so should perch frequently in sun patches throughout the

day. The nymphalid butterfly *Polygonia comma*, a forest species occupying sun patches during midafternoon, follows these as they move and has no predictable start time (unpublished data). *P. comma* leaves territories more predictably later in the afternoon as the sunlight becomes too weak to keep them warm.

V. atalanta (Bitzer and Shaw, 1979) perches at highly predictable times each day under most types of weather. Start time variations correlate with cloud cover or T_s , rather than with early intruder frequency, suggesting *V. atalanta*'s start time is highly climate-dependent. On the other hand, the mean interval between early arrivals decreases at higher T_a , which is consistent with Wickman and Wiklund's (1983) findings that more and more *Pararge aegeria* males switch to patrolling as T_a rises. *V. atalanta* territorial behavior may be density-dependent to some extent, but such effects may appear more strongly as variations in interaction duration or outcome, occupant turnover rate, or total number of occupied territories (Bitzer and Shaw, in preparation). We also note that unlike *P. aegeria* (Wickman and Wiklund 1983), *V. atalanta* never abandoned territorial behavior completely at the highest levels of either T_a or early interaction frequency.

We also believe that neither a decrease in unmated females (Dennis and Williams, 1987; Rutowski, 1991) nor declining energy supplies (Dennis and Williams, 1987) significantly affect when *V. atalanta* males start perching. If either did, start times should be much more variable and depend upon the degree of competition for food or mates. For this reason, Rutowski (1991) suggests that the satyrid *Coenonympha pamphilus* may defend sunspots later in the day because density of receptive females declines, rather than the T_a -induced need to bask which Wickman (1985a) suggests.

Since start times are so highly correlated with T_a , we doubt that the density of unmated females would decrease earlier so consistently on cooler days. Butterflies have fewer hours to patrol during mid-day on cooler days (Vielmetter, 1958; Wickman, 1985a), and females may actually emerge later on cooler days (Iwasa and Obara, 1989), which would delay the entire activity schedule were it driven mainly by female density. Baker (1972) found that *Inachis io* and *Aglaia urticae* eclosed in the morning, but copulated only after roosting. *V. atalanta* may likewise copulate only in late afternoon, although captive females typically eclosed before 0700 (unpublished data). If so, *V. atalanta* start time would not depend upon female density at all.

We also doubt that *V. atalanta* perches when its energy reserves decline, because it, like *Ochlodes venata* (Dennis and Williams, 1987), flies vigorous interactions matching or exceeding the demands of patrolling. *V. atalanta* thus seems to be a climate-dependent perching species which responds to a climate-modulated circadian rhythm.

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CHAPTER 2. TERRITORIAL BEHAVIOR OF THE RED ADMIRAL,
Vanessa atalanta (LEPIDOPTERA: NYMPHALIDAE):
 II. THE ROLE OF CLIMATIC FACTORS AND INTERACTION FREQUENCY
 ON TERRITORIAL END DANCE

A paper to be submitted to the Journal of Insect Behavior

Royce J. Bitzer^{1,2} and Kenneth C. Shaw¹

ABSTRACT

We examined the relative importance of climatic factors and population density to time of the last territorial interaction (end dance time) of *Vanessa atalanta* males. End dance time varies with solar altitude, which determines radiation (R_{\odot}) levels, and therefore varies with seasons. We removed seasonal effects by converting end dance times to corresponding solar altitudes. End dance solar altitude correlates primarily with ambient temperature (T_a) and secondarily with interaction frequency (FREQ), regardless of cloud cover. However, overcast cloud cover resulted in earlier end dance times as expected from reduced solar radiation (R_{\odot}) levels, which were similar at end dance times on both sunny and overcast days. R_{\odot} may directly affect end dance time by affecting equilibrium body temperature (T_b) of flying vagrant males. End dance time nevertheless occurred over a wide range of equilibrium T_b ; these data suggested that end dance time was limited by oncoming darkness as light (diffuse R_{\odot}) levels fell

¹Graduate student and Associate Professor, respectively,
 Department of Zoology and Genetics, Iowa State University.

²Author for correspondence.

near sunset. Although an increase in wind velocity (V_w), which should lower T_b , resulted in earlier end dance, FREQ was not affected. FREQ was correlated not only with T_a and cloud cover, but also with variations in end dance time, suggesting that male population density influences how *V. atalanta* males respond to climatic factors around end dance time. We conclude that the time of the last *V. atalanta* occupant-intruder interaction depends upon both climatic factors and population density.

INTRODUCTION

Climatic factors must permit butterflies to attain body temperatures high enough for vigorous flight (Heinrich, 1981; 1986; Tsuji *et al.*, 1986; Rutowski *et al.*, 1994). Biological factors, such as density of conspecific males (Wickman and Wiklund, 1983; Alcock, 1985; Iwasa and Obara, 1989; Rutowski, 1991) or interspecific competition from other butterflies (Bitzer and Shaw, 1983), may affect whether or when males seek conspecific females while flying (patrolling) and/or while perching (Alcock, 1985; Dennis and Williams, 1987; Rutowski, 1991; Wickman and Wiklund, 1983; Wickman, 1985a; 1985b; 1988). Thermoregulatory strategies are often combined opportunistically with mate-location (Douwes, 1976; Shreeve, 1984; Dennis and Shreeve, 1988; Rutowski *et al.*, 1994; Bitzer and Shaw, 1995). Studies have shown that mating strategy in some species changes as both climatic and biological factors vary (Wickman and Wiklund, 1983; Wickman, 1985a; 1985b; 1988).

If climatic factors are predictable over the course of the day, so might be the periods when butterflies initiate or terminate perching in mating territories. We have examined the relative importance of climatic factors and early

interaction frequency (a measure of population density) to the territorial start time of *Vanessa atalanta* (Bitzer and Shaw, 1995) and found start time to be highly correlated with ambient temperature (T_a), solar radiation (R_{\odot}), substrate temperature (T_s), and cloud cover.

We have also examined the extent to which climatic factors and interaction frequency affect territorial end time [when males leave the territory to roost for the night, (Bitzer and Shaw, in preparation.)] and the time of end dance (the last interaction between the territorial male and the final intruder), the subject of this study.

Vielmetter (1958) found that ambient temperature (T_a) and solar radiation (R_{\odot}) interacted inversely to cause the non-territorial nymphalid butterfly *Argynnis paphia* to switch between continuous flight and stationary basking at a critical body temperature (T_b) of 34.2°C. A similar relationship was found for *V. atalanta* start time on sunny days (Bitzer and Shaw, 1995). There is also a lower critical T_b (23.4°C) at which *A. paphia* decamps from its perch and flies up into nearby trees to roost (Vielmetter, 1958). Douwes (1976) found similar relationships for *Heodes virgaureae*. If the end dance time of *V. atalanta* likewise depends upon T_a and R_{\odot} , it may occur at a critical T_b at which vagrant *V. atalanta* males can no longer fly between territories.

The solar radiation level at a given time of day varies with seasonal solar declination. We have shown that the start time of *V. atalanta* varies correspondingly with the seasons (Bitzer and Shaw, 1995), as have Swanson (1979; personal communication) and Brown and Alcock (1991), with the latest start times occurring in mid-summer. We will present a similar seasonal model of *V. atalanta* end dance time.

V. atalanta males respond to solid overcast by perching in territories later than they do on clear days, rather than earlier as one would expect from the corresponding solar radiation levels (Bitzer and Shaw, 1995). This behavior might result from lower substrate temperature (T_s) on overcast days (Bitzer and Shaw, 1995), or because males may continue to benefit from the patrolling strategy later in the day under overcast skies (Bitzer and Shaw, 1995, Dennis and Williams, 1987). We expect substrate temperature to be less important to flying intruders than it is to perched occupants. How, then, might overcast skies affect the time of end dance? Do flying *V. atalanta* males simply react to the solar radiation level whatever the cloud conditions?

Since flying butterflies are more susceptible to wind than are perched ones, end dance time, unlike start time (Bitzer and Shaw, 1995), may depend upon wind velocity. Excess temperature ($T_{ex}=T_b-T_a$) varies directly with T_a and R_\odot , but inversely as the square root of wind velocity (V_w) (Digby, 1955, Tsuji *et al.*, 1986), whereas relaxation times for equilibrium T_b depend directly on T_a , R_\odot , and inversely on V_w (Dennis, 1993).

If biological factors such as population density of conspecific males are important, butterflies' activity schedules may vary more than one might expect from climatic factors alone. A higher density of conspecific males suggests more territorial scramble competition, which could lead to a spillover of flying males persisting later into the territorial period. On the other hand, males might stop interacting earlier when the number of perched males/territory becomes very high (Alcock and O'Neill, 1986). Iwasa and Obara's (1989) game theory model suggests that when the numbers of receptive females are similar, both the start and end dance times of *V. atalanta* males should occur earlier on days when

more males are patrolling for females. The number of remaining receptive females would drop low enough earlier in the day to trigger males to switch gradually from patrolling to perching, and finally to abandon the patrolling strategy entirely at end dance time. We thus correlated end dance time with both the interaction frequency (FREQ) and the maximum number of joint occupants (MAX) in the territory that day.

We identify correlations of several climatic and population density variables with territorial end dance time and determine their relative importance. We also establish models to which end dance time of other populations or species might be compared. These findings will provide a basis for future experimental work on end dance time.

MATERIALS AND METHODS

Butterflies were observed on the Iowa State University campus between April and September from 1987-1992. We recorded a total of 204 end dances. These were defined as the time when the last *V. atalanta* male intruder flew through a territory, interacted with the occupant, and then separated from the occupant. On 2 days, the last intruder flew through after all occupants had already left, so the time when this butterfly passed over the territory was counted as an end dance. We analyzed data from 198 end dances for which we had complete information on ambient temperature (T_a), interaction frequency (FREQ), and maximum number of joint occupants (MAX), including one primary and up to three secondary occupants. For 94 end dances recorded between 1989 and 1992, we also measured solar radiation (R_{\odot}), wind velocity (V_w), and substrate temperature (T_s). Two observations when no intruders arrived

(FREQ=0) were discarded from two analyses (n=196) using base-10 logarithms of FREQ. Both were from overcast days.

We observed end dances at 10 optimal [most frequently occupied, (Bitzer and Shaw, 1979)] territorial sites on campus, most often at Territories 11 (123 observations) and 13 (52 obs.) described in Bitzer and Shaw (1995). On 11 days, we recorded end dances in both Territory 11 and Territory 13. Sunlight fell in these areas most strongly before 1600h CST, then became increasingly patchier, and was gone by 1910-1930h.

We used both FREQ and MAX to estimate population density during the territorial period. We calculated FREQ by dividing the total number of intruders which interacted with occupants by the duration of the territorial period. For vagrant butterflies to become secondary occupants, they had to remain in the territory after one bout of interactions.

End dance and other interaction times were recorded to the nearest second (Central Standard Time) with a digital quartz clock/stopwatch set by time signals from the National Bureau of Standards (NBS) radio station WWV, and were converted to four-place decimal equivalents. Solar altitude corresponding to each end dance time was calculated as in Campbell (1977, p. 53). Latitude (42°01'38"N) and longitude (93°38'42"W) of the territorial sites were taken from a USGS topographical map. Solar declination (δ , angular distance of the sun north or south of the equator) and ephemeris time of solar noon were taken from the *Astronomical Almanac* (1987-1992). Time of solar noon was corrected for longitude. We then subtracted 12h from this corrected value to obtain the solar noon variation (ϵ), the difference between CST and local solar transit time. Solar altitude values were uncorrected for atmospheric refraction.

Ambient temperature (T_a), cloud cover, and wind velocity (V_w) were recorded from 1987 through 1992 as in Bitzer and Shaw (1995). Substrate temperature (T_s) was recorded in ground-based territories on 94 days from 1989 through 1992 as in Bitzer and Shaw (1995). We also used an Everest Interscience, Inc. Model 120 handheld infrared thermometer during 1991 and 1992 to read T_s of perch sites in both territories. These readings varied no more than 0.3°C from thermocouple readings of the same spots. Emissivity of soil and stone was assumed to be 0.95; that of vegetation, 0.98, in accord with standard practice (see Monteith and Unsworth, 1990, pp. 81-85).

We estimated equilibrium body temperature (T_b) from 1989 through 1992 as in Bitzer and Shaw (1995). We also recorded T_b of a dead butterfly suspended in flight position at 160 cm during 1992. We kept the pyranometer and the T_s and T_b probes within a 60-cm circle under similar levels of solar radiation, with no probes shading any others.

Multiple regression and analysis of covariance (ANCOVA) were used to analyze statistical models unless one or more of the independent variables were correlated with each other. When they were, we used principal components analysis to identify distinct groups of continuous variables as well as linear combinations of the original variables which had the smallest variance. Principal components derived from the continuous variables were then analyzed in ANCOVA models containing the discrete variables of cloud cover and territory site. Simple correlations were used to examine and graph relationships between end dance and some of the independent variables.

RESULTS

Variables Correlated with End Dance Time

End Dance Varies with Ambient Temperature, Time of Year, and Interaction Frequency

End dance time was correlated with T_a , occurring later when T_a was higher (Fig. 1, $R^2=0.36$, $F=111.61$, $P<0.0001$, $n=198$). End dance time increased linearly by 7.57 min for each additional 1°C of T_a .

Intruders stopped arriving 20-50 min earlier at the same T_a in early May and in August through September than they did from mid-May through July (Fig. 1). Seasonal changes in both solar declination (δ) and time of solar noon (ϵ) correlated with end dance time (Table I). End dance times for any particular T_a were earlier when δ was lower, and also followed seasonal variations in ϵ . Accounting for both δ and ϵ explained an additional 17% of the residual variability in the first model ($R^2=0.53$, $F=73.74$, $P<0.0001$, $n=198$).

Interaction frequency (FREQ; Table I) was as strongly related to end dance time as was time of solar noon. End dance time was 0.72 min (43 s) later per unit increase in interaction frequency. This compares with +5.22 min/ $^\circ\text{C}$ and +4.68 min/degree of solar declination in the full model.

When the relationship of end dance time to T_a was partitioned by cloud cover (Fig. 2), we found that end dance time changed more rapidly with T_a under overcast than under clear skies. The difference in end dance time between clear and overcast days was greater when T_a was lower (Fig. 2).

Similar effects of cloud cover were evident when end dance time was expressed as the corresponding solar altitude. Regressing the end dance solar altitude (EDSA) against T_a (Fig. 3) combined end dance time, δ , and ϵ into a

Figure 1. Relationship of ambient temperature (T_a) and solar declination (δ) to end dance time (hours CST). Sky conditions: + : Clear sky; O: Cirroform cloudiness; ∇ : Cumuliform cloudiness; \blacklozenge : Overcast. ————— : Regression line for all 198 observations (End dance time = $15\text{h}.56 + 0.13 T_a$). - - - - - : End dance time line for 21 June ($\delta = +23^\circ.4433$). : Line for 21 April/August ($\delta = +12^\circ$). To simplify the graph, time of solar noon was set at 12h 17 min 03s (12h.2841), near the mean value for all data; thus $\epsilon = 17 \text{ min } 03\text{s}$ (0h.2841). End dance time = $13\text{h}.85 + 0.101T_a + 0.082\delta + 2.55\epsilon$: Start time vs. T_a from Bitzer and Shaw (1995).

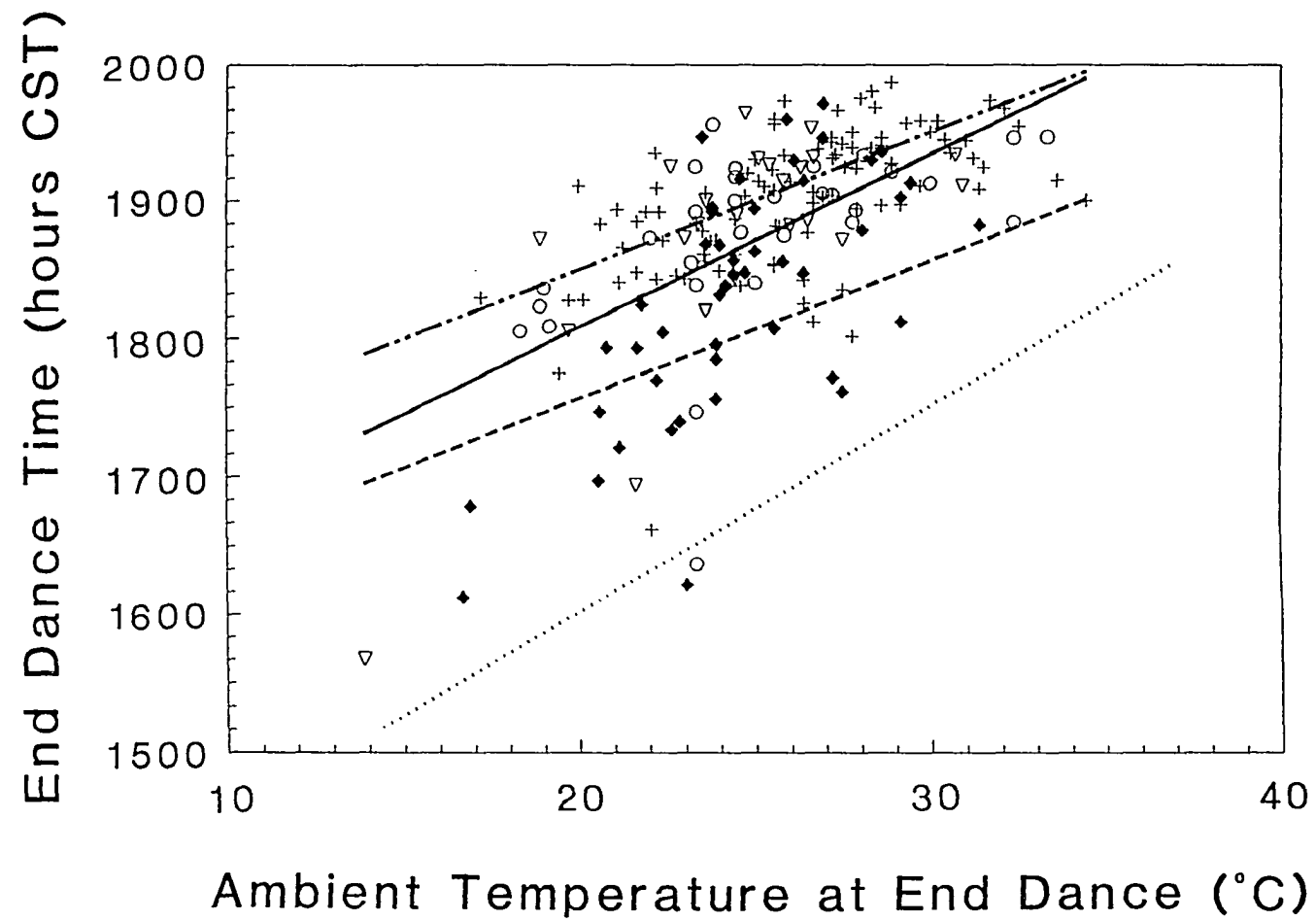


Table I. The Effects of Ambient Temperature, Solar Declination, Solar Noon Variation, Interaction Frequency, and Cloud Cover upon End Dance Time^a.

Source	df	SS	<i>F</i>	<i>P</i>
Ambient temp. (T_a)	1	15.47	81.08	<0.0001
Declination (δ)	1	13.01	68.17	<0.0001
Solar noon variation (ϵ)	1	4.04	21.16	<0.0001
Interaction frequency (FREQ)	1	4.18	21.89	<0.0001
Cloud cover	3	7.21	12.60	<0.0001

Cloud cover	Adjusted mean ETSA	C. cover difference	Different from clear? <i>t</i>	<i>P</i>
Overcast	18h.43	-0h.48	-6.06	<0.0001
Cumuliform	18h.76	-0h.14	-1.41	0.1597
Cirroform	18h.83	-0h.08	-0.86	0.3906
Clear	18h.91	0	-	-

^aEnd dance time = $14\text{h.}25 + 0.087T_a + 0.078\delta + 2.58\epsilon + 0.012(\text{FREQ}) + \text{Cloud cover difference}$. $R^2 = 0.66$, $F = 52.17$, $P < 0.0001$, $n = 198$, 7 treatment df.

^bStandard time of solar transit - 12 h.

Figure 2. Relationship of ambient temperature (T_a) to end dance time (hours CST), by cloud cover. Sky conditions are indicated as in Fig. 1. — : End dance time line for clear skies (End dance = $16h.64 + 0.09T_a$, $R^2=0.35$, $n=97$). - - - - - : Cirroform cloudiness ($16h.52 + 0.09T_a$, $R^2=0.27$, $n=30$). - . - . - . : Cumuliform cloudiness ($14h.37 + 0.18T_a$, $R^2=0.54$, $n=24$). - - - - - : Overcast ($13h.93 + 0.18T_a$, $R^2=0.41$, $n=47$). : Start time line as in Fig. 1.

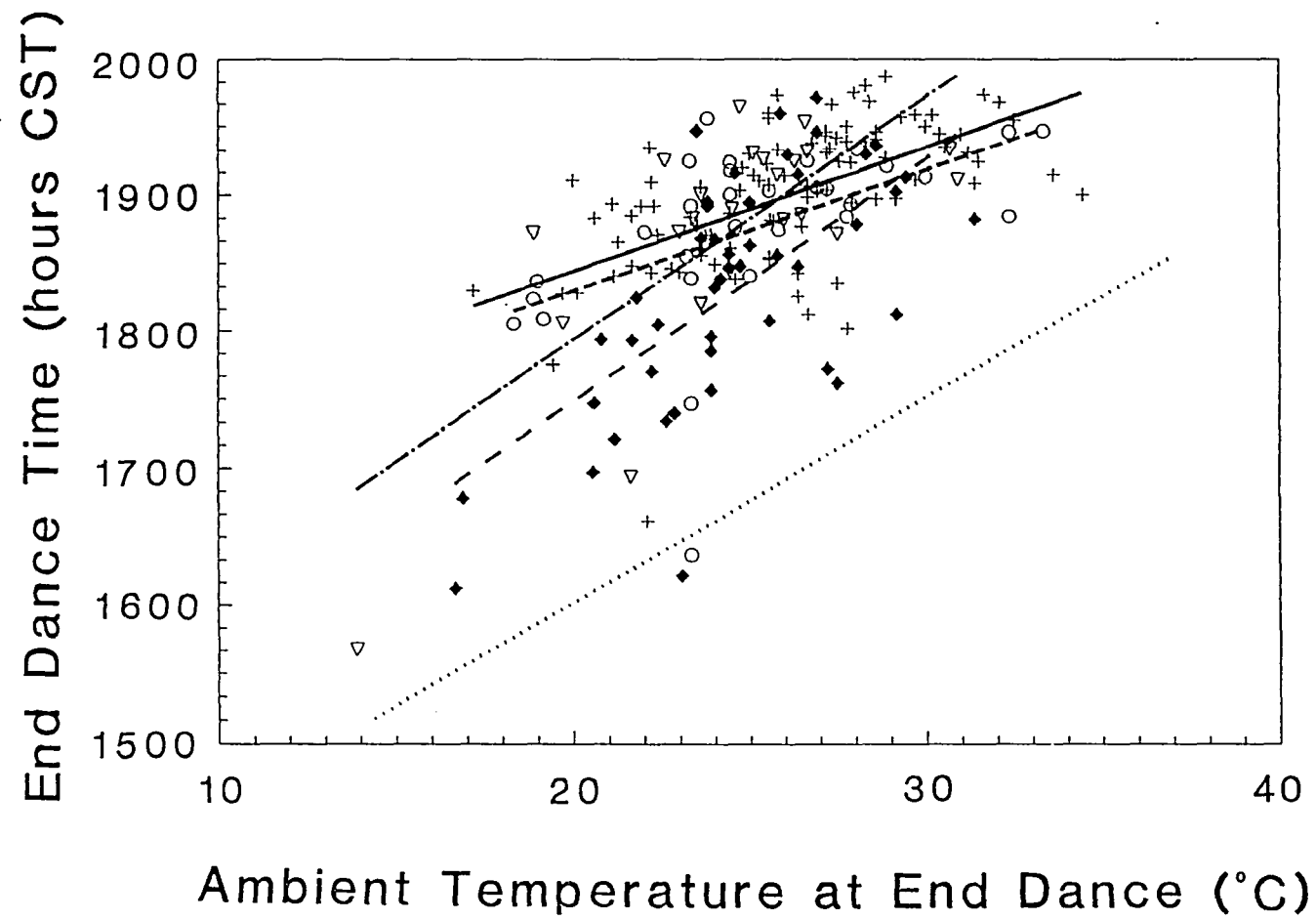
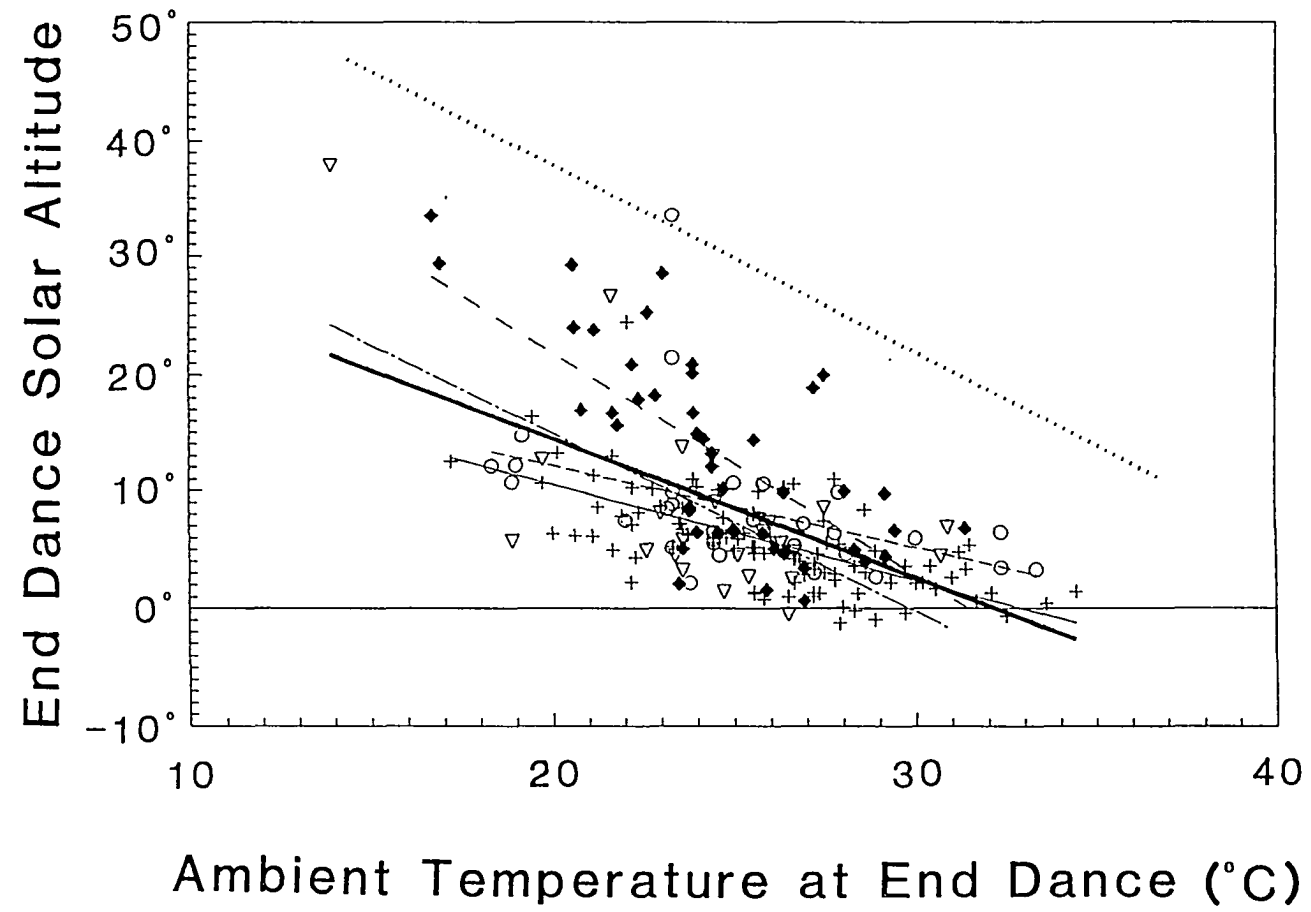


Figure 3. Relationship of ambient temperature (T_a) to end dance time (expressed as the corresponding solar altitude, EDSA). Sky conditions are indicated as in Fig. 1. — : Regression line for all 198 observations ($\text{EDSA} = 38^\circ.22 - 1.19T_a$). — : Clear sky: $\text{EDSA} = 26^\circ.83 - 0.82T_a$, $n=97$. - - - - - : Cirroform cloudiness: $\text{EDSA} = 26^\circ.16 - 0.70T_a$, $n=30$. - . - . - . : Cumuliform cloudiness: $\text{EDSA} = 45^\circ.37 - 1.52T_a$, $n=24$. - - - - - : Overcast: $\text{EDSA} = 60^\circ.10 - 1.91T_a$, $n=47$: Start time solar altitude vs. T_a from Bitzer and Shaw (1995).



single factor, yielding a model ($R^2=0.36$, $F=109.19$, $P<0.0001$, $n=198$) analogous to Vielmetter's (1958). The sun averaged $1^\circ.19$ lower (ca. 6.62 m later) at end dance time for each increase of 1°C . End dance time was more predictable for sunny days ($R^2=0.43$, $F=72.40$, $P<0.0001$, $n=97$), overcast days ($R^2=0.49$, $F=43.53$, $P<0.0001$, $n=47$), and cumuliform-clouded days ($R^2=0.43$, $F=16.47$, $P=0.0005$, $n=24$) than it was for all sky conditions combined, suggesting that cloud cover produced considerable variability in the latter model. There was no significant difference between clear and cirroform days ($t=-1.43$, $P=0.15$), between cirroform and cumuliform days ($t=-0.066$, $P=0.95$), or between clear and cumuliform days ($t=-1.39$, $P=0.16$).

V. atalanta males on sunny days stop flying based on an inverse relationship between T_a and solar altitude, the latter determining the amount of solar radiation (see Vielmetter 1958). Solar radiation (R_\odot) on clear afternoons decreases linearly with solar altitude, except near sunset when the sun is less than 10° up (Campbell, 1977, p. 56). Plotting end dance time of territorial butterflies as a solar altitude value allows one to compare activity schedules of different populations and different species located in various latitudes.

*Correlation of Ambient Temperature, Interaction Frequency
or Maximum Number of Joint Occupants, Cloud Cover,
and Year with EDSA*

These two models used all 198 observations from 1987-1992. Simple correlations of T_a , FREQ, and MAX showed that FREQ and MAX were positively correlated ($r=0.44$, $P<0.0001$, $n=198$). T_a was not correlated with either FREQ ($r=0.12$, $P=0.0976$) or MAX ($r=0.11$, $P=0.1224$). Because FREQ and MAX were confounded, the two were analyzed in separate ANCOVA models.

EDSA decreased (end dance was later) as both T_a and population density factors increased (Figs. 3-5).

The first ANCOVA model including FREQ showed that T_a , FREQ, cloud cover, and year all correlated with EDSA, and therefore with end dance time (Table II, ANCOVA with significant variables). Comparing the three types of cloud cover with clear skies showed that butterflies stopped flying earlier (EDSA was higher) on overcast afternoons than on clear ones (Table II). EDSA's under cumuliform and cirroform clouds, however, did not differ from those under clear skies. EDSA under overcast conditions was higher than under both cumuliform ($t=3.47$, $P=0.0006$) and cirroform ($t=3.68$, $P=0.0003$) conditions.

The end dance time- T_a relationship varied from year to year, averaging the earliest in 1988 and 1989, intermediate in 1987 and 1992, and latest in 1990 and 1991. 1990 end dance times were later than those of the preceding three years (range of t : 2.19-3.51, $P=0.0296$ to 0.0006), and 1991 end dance times were later than those of 1989 ($t=2.43$, $P=0.0159$).

End Dance Time, Ambient Temperature, and Arrival Frequency

End dance time is later when more flying butterflies are active during the territorial period. EDSA averaged $0^\circ.12$ lower (ca. 40s later) for each additional interaction/hour (Fig. 4). EDSA is also correlated with \log_{10} FREQ over all sky conditions ($R^2=0.21$, $F=52.34$, $P<0.0001$, $n=196$). This relationship is most pronounced on overcast days, least pronounced on clear days (Fig. 5). The higher the interaction frequency, the smaller is the secondary correlation with cloud cover (Fig. 5). The highest rates of interaction correlate similarly with the latest end dances, regardless of cloud cover (Fig. 5).

Figure 4. Relationship of ambient temperature (T_a) and interaction frequency (FREQ) to end dance time (expressed as the corresponding solar altitude, EDSA). Sky conditions are indicated as in Fig. 1.

———— : Regression line for all 198 observations ($EDSA = 38^\circ.22 - 1.19T_a$).

———— : Estimated schedule as $FREQ \rightarrow 0$ interactions/h. - - - - - : FREQ = 10.

- . - . - . : FREQ = 50. - - - - - : FREQ = 100. $EDSA = 38^\circ.38 - 1.12T_a - 0.14(FREQ)$.

..... : Start time solar altitude vs. T_a from Bitzer and Shaw (1995).

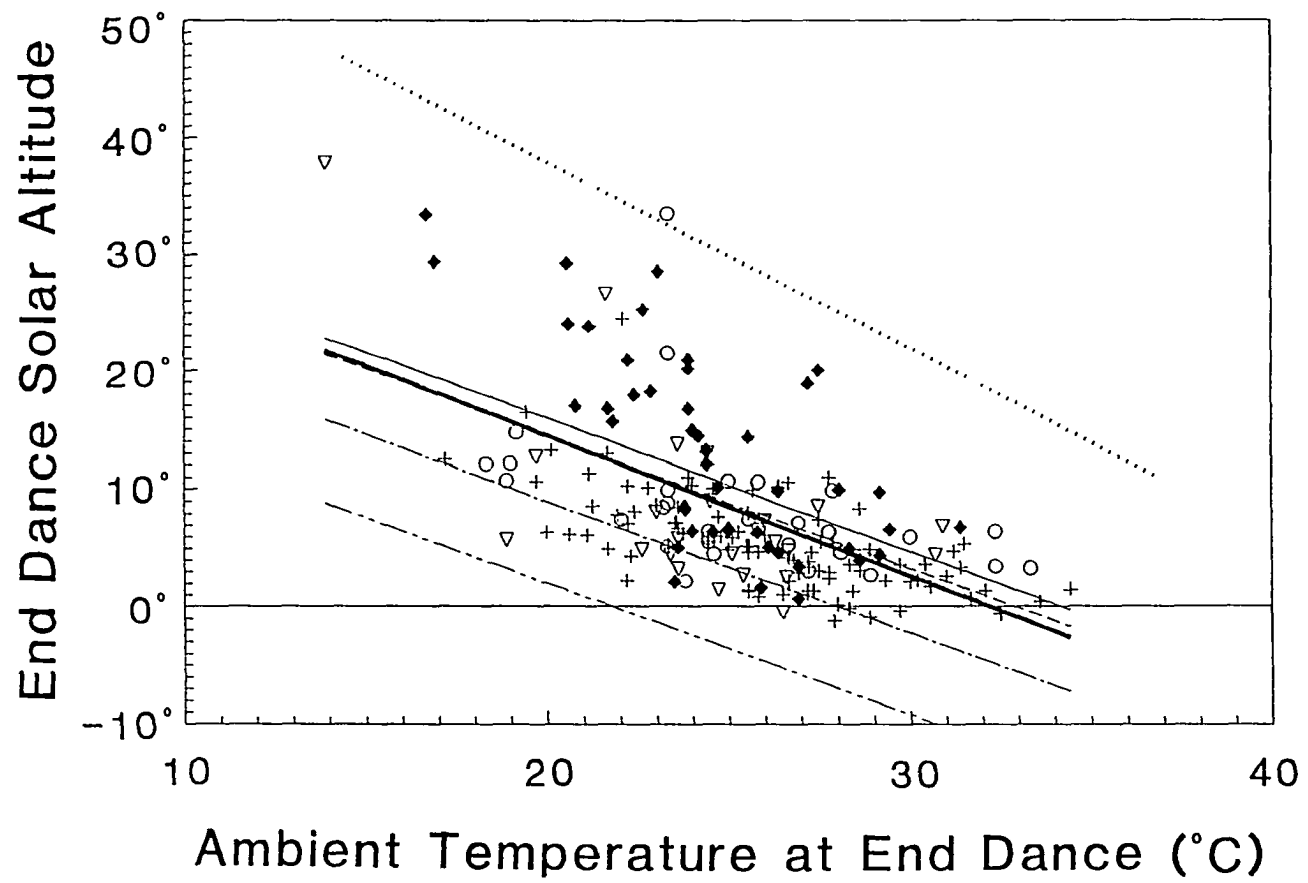


Figure 5. Relationship of interaction frequency (FREQ) to end dance time (expressed as the corresponding solar altitude). Sky conditions and the corresponding regression lines are indicated as in Fig. 2.

All conditions: $\text{EDSA} = 14^{\circ}.90 - 7.48 \log_{10} \text{FREQ}$, $n=196$. Clear sky: $\text{EDSA} = 10^{\circ}.01 - 4.38 \log_{10} \text{FREQ}$, $n=97$. Cirroform cloudiness: $\text{EDSA} = 14^{\circ}.12 - 6.33 \log_{10} \text{FREQ}$, $n=30$. Cumuliform cloudiness: $\text{EDSA} = 16^{\circ}.92 - 9.72 \log_{10} \text{FREQ}$, $n=24$. Overcast: $\text{EDSA} = 19^{\circ}.61 - 8.79 \log_{10} \text{FREQ}$, $n=45$.

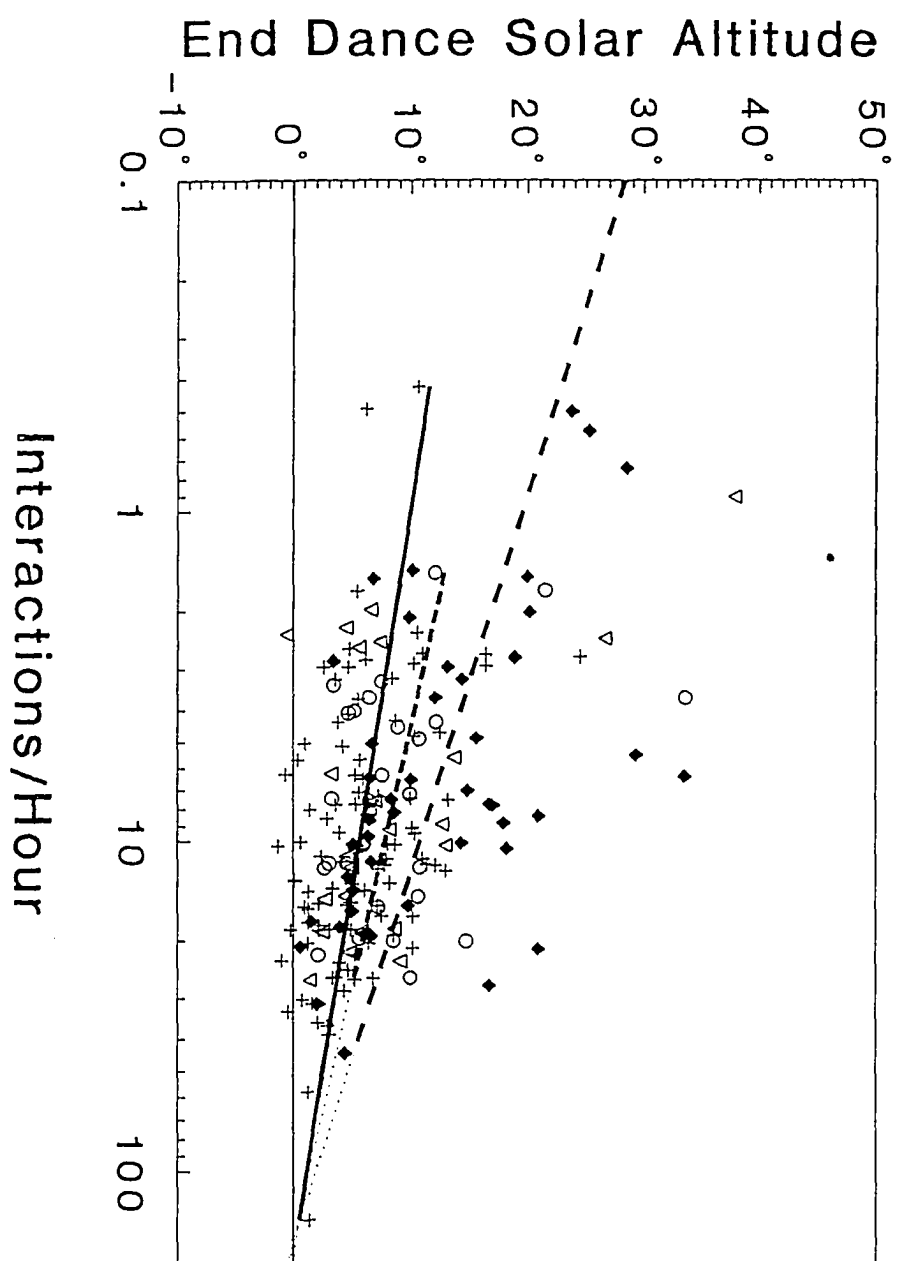


Table II. The Effects of Ambient Temperature, Interaction Frequency, Cloud Cover, and Year upon End Dance Time (Expressed as Solar Altitude^a).

Source	df	SS	<i>F</i>	<i>P</i>
Ambient temp. (T_a)	1	2079.71	92.41	<0.0001
Interaction frequency (FREQ)	1	444.47	19.75	<0.0001
Cloud cover	3	293.02	13.02	<0.0001
Year	5	65.39	2.91	0.0150

Cloud cover	Adjusted mean EDSA	C. cover difference	Different from clear? <i>t</i>	<i>P</i>
Overcast	11°.93	5°.47	6.19	<0.0001
Cumuliform	7°.68	1°.22	1.07	0.2849
Cirroform	7°.72	1°.25	1.23	0.2211
Clear	6°.47	0	-	-

Year	Adjusted mean EDSA	Year difference	Different from 1992? <i>t</i>	<i>P</i>
1987	8°.87	0°.67	0.42	0.6782
1988	9°.12	0°.92	0.56	0.5793
1989	10°.58	2°.38	1.45	0.1476
1990	6°.46	-1°.73	-1.08	0.2814
1991	7°.48	-0°.72	-0.42	0.6723
1992	8°.20	0	-	-

^aEDSA = $34°.41 - 1.05T_a - 0.12(\text{FREQ}) + \text{cloud cover difference} + \text{year difference}$. $R^2 = 0.56$, $F = 23.42$, $P < 0.0001$, $n = 198$, 10 treatment df.

Arrival frequency itself tends weakly to be higher on warmer overcast days ($\text{FREQ} = -13.88 + 0.96 T_a$; $R^2=0.11$, $F=5.37$, $P=0.0251$, $n=47$). On clear days as well as for all conditions, interaction frequency peaks when end dance T_a is ca. 27.0-27.5°C (Fig. 6).

Correlations With Maximum Number of Joint Occupants

When the maximum simultaneous occupant number (MAX) was used instead of FREQ, the relative importance of T_a , types of cloud cover, and year of observation were similar. Higher MAX correlated with later end dance times ($F=5.02$, $P=0.0007$), which were latest when MAX=4, ca. 37 min earlier when MAX was 2-3, and ca. 47 min earlier when MAX=1.

Principal Components Analysis of Interaction Frequency, Maximum Number of Simultaneous Occupants, Ambient Temperature, Solar Radiation, Substrate Temperature, and Wind Velocity

This model used 94 observations from 1989-1992. Simple correlations of FREQ, MAX, T_a , R_{\odot} , T_s , and V_w showed correlations between FREQ and MAX ($r=0.43$, $P<0.0001$), FREQ and T_a ($r=0.23$, $P=0.0237$), MAX and T_a ($r=0.27$, $P=0.0098$), T_a and R_{\odot} ($r=-0.45$, $P<0.0001$), FREQ and T_s ($r=0.25$, $P=0.0164$), MAX and T_s ($r=0.22$, $P=0.0356$), T_s and R_{\odot} ($r=-0.23$, $P=0.0270$), and T_a and T_s ($r=0.73$, $P<0.0001$). In this analysis, unlike the preceding one, population density and T_a effects were confounded, as were some other variables. We therefore used principal components analysis.

Principal components analysis showed that the eigenvalues of the first three principal components contained 75.3% of the total variance (Table III). Prin 6 contained only 3.2% of the total variance, and was thus used to determine relative importance of the six continuous variables as in Gaugler and Schutz

Figure 6. Correlation of ambient temperature (T_a) at end dance with the common logarithm of daily interaction frequency ($\log_{10}\text{FREQ}$). Sky conditions are indicated as in Fig. 2. Mean arrival intervals: — : For all sky conditions: $\log_{10}\text{FREQ} = -0.0047 (T_a)^2 + 0.26 T_a - 2.59$ ($R^2=0.074$, $F=7.69$, $P=0.0006$, $n=196$). — : For clear skies: $\log_{10}\text{FREQ} = -0.0076 (T_a)^2 + 0.41 T_a - 4.42$ ($R^2=0.10$, $F=5.35$, $P=0.0063$, $n=97$).

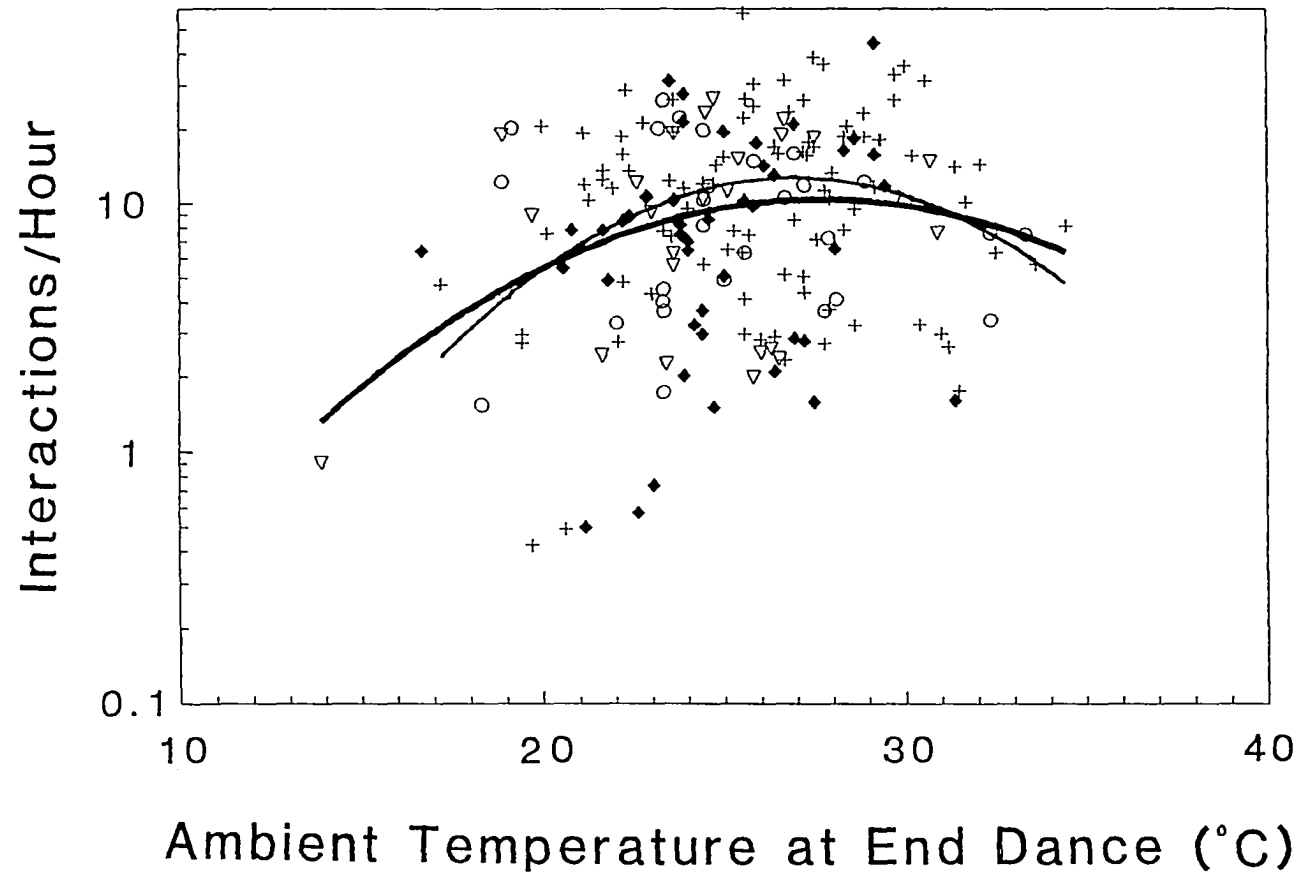


Table III. Principal Components Analysis of End Dance Time: Eigenvalues and Proportion of Variance. Continuous independent variables include ambient temperature, solar radiation, substrate temperature, wind velocity, interaction frequency, and maximum number of joint occupants.

Principal component	Eigenvalue ^a	Proportion of variance ^b
1	2.290	0.382
2	1.170	0.195
3	1.053	0.176
4	0.743	0.124
5	0.547	0.091
6	0.197	0.032

^aEigenvalues represent variance of principal component.

^bProportion of total variance included in principal component.

(1989). The eigenvectors of the variables (Table IV) indicate that T_a and T_s effects lie mainly in Prin 1, FREQ and MAX effects lie mainly in Prin 2, while Prin 3 contains mainly R_{\odot} and V_w effects.

Prin 1, 2 and 3 were then analyzed in an ANCOVA along with the class variables of cloud cover, year, and territory site (Table V). Prin 1 showed that EDSA varied with both T_a and T_s . Prin 2, strongly representing the population density factors, was insignificant. Prin 3 indicated that EDSA varied with both V_w and R_{\odot} . Prin 6 indicates that T_a and T_s (Prin 1) are the strongest predictors of EDSA (end dance was later when T_a was higher and T_s was lower). R_{\odot} and V_w (Prin 3) were weaker predictors (end dance was later when R_{\odot} was higher and V_w was lower), and FREQ and MAX (Prin 2) were not significant predictors of EDSA in this analysis. This result contradicts that of the previous ANCOVA (Table II), which included fewer climatic factors. We found similar results when we analyzed each sky condition separately, or when we used the square root of V_w , or \log_{10} FREQ.

EDSA was higher (end dance was earlier) for overcast compared with clear conditions (Table V), but as before, EDSA's for either cumuliiform or cirroform skies were not significantly different from clear skies, but were significantly different from overcast skies (cumuliiform: $t=3.31$, $P=0.0014$; cirroform: $t=3.32$, $P=0.0014$).

*Relationship between Ambient Temperature, Solar Radiation
and Body Temperature at End Dance Time*

Plotting R_{\odot} against T_a at end dance time (Fig. 7) showed that vagrant butterflies stop flying when R_{\odot} and T_a decline to critical levels, whatever the cloud cover. An ANCOVA model for the four sky conditions (Table VI) indicated

Table IV. Principal Components Analysis of End Dance Time: Eigenvectors of Individual Variables for Principal Components 1, 2, 3, and 6.

Principal component	1	2	3	6
Variable				
Ambient temperature (T_a)	0.558	-0.380	0.077	0.726
Solar radiation (R_{\odot})	-0.372	0.205	0.502	0.290
Substrate temperature (T_s)	0.519	-0.268	0.050	-0.582
Wind velocity (V_w)	-0.104	-0.454	0.746	-0.182
Interaction frequency (FREQ)	0.383	0.529	0.139	0.064
Maximum no. of occupants (MAX)	0.351	0.506	0.405	-0.111

Table V. Principal Components Analysis of End Dance Time: End Dance Solar Altitude^a vs. Principal Components 1, 2, and 3, Cloud Cover, Year, and Territory Site.

Source	df	SS	<i>F</i>	<i>P</i>
Prin 1	1	929.51	55.09	<0.0001
Prin 2	1	9.65	0.57	0.4518
Prin 3	1	115.37	6.84	0.0107
Cloud cover	3	374.76	7.40	0.0002
Year	3	65.46	1.29	0.2825
Territory site	4	64.17	0.95	0.4393

Cloud cover	Adjusted mean EDSA	C. cover difference	Different from clear? <i>t</i>	<i>P</i>
Overcast	12°.92	5°.42	4.49	<0.0001
Cumuliform	8°.42	0°.91	0.76	0.4466
Cirroform	7°.45	-0°.05	-0.04	0.9715
Clear	7°.51	0	-	-

^aEDSA = $11^{\circ}.26 - 2.39(\text{Prin } 1) + 1.22(\text{Prin } 3) + \text{cloud cover difference}$. $R^2 = 0.63$, $F = 10.42$, $P < 0.0001$, $n = 94$, 13 treatment df.

Prin 1 = $0.38(\text{FREQ}-11.49)/9.35 + 0.35(\text{MAX}-1.4574)/0.63 + 0.56(T_a-24.93)/3.13 - 0.37(R_{\odot}-26.43)/35.77 + 0.52(T_s-26.43)/3.64 - 0.10(V_w-1.13)/0.67$ (Mainly ambient and substrate temperatures).

Prin 2 = $0.53(\text{FREQ}-11.49)/9.35 + 0.51(\text{MAX}-1.4574)/0.63 - 0.38(T_a-24.93)/3.13 + 0.21(R_{\odot}-26.43)/35.77 - 0.27(T_s-26.43)/3.64 - 0.45(V_w-1.13)/0.67$ (Mainly population density factors).

Prin 3 = $0.14(\text{FREQ}-11.49)/9.35 + 0.41(\text{MAX}-1.4574)/0.63 + 0.08(T_a-24.93)/3.13 + 0.50(R_{\odot}-26.43)/35.77 + 0.05(T_s-26.43)/3.64 + 0.75(V_w-1.13)/0.67$ (Mainly solar radiation and wind velocity).

Figure 7. Correlation of ambient temperature (T_a) and solar radiation (R_{\odot}) at end dance time on 94 days.

Sky conditions and the corresponding regression lines are indicated as in Fig. 2. Solid sloping contours are isotherms ($^{\circ}\text{C}$) of equilibrium body temperature (T_b) of freshly-killed *V. atalanta* males in dorsal basking position, measured at 1-min intervals during the territorial period on 10 days in 1992 ($n=1013$). Dashed contours are the corresponding T_b isotherms for freshly-killed males suspended in flight position at 160 cm. After locating T_a and R_{\odot} on the axes, read the predicted T_b from the diagonal isotherm contours. *V. atalanta* end dance: Clear sky, linear: $R_{\odot} = 184.07 \text{ W/m}^2 - 6.18T_a$; $R^2=0.26$, $n=41$. Clear sky, exponential: $R_{\odot} = 2606.64e^{-0.204T_a}$; $R^2=0.46$. Cirroform cloudiness: $R_{\odot} = 49.60 \text{ W/m}^2 - 1.45T_a$; $R^2=0.55$, $n=10$. Cumuliform cloudiness: $R_{\odot} = 128.75 \text{ W/m}^2 - 3.99T_a$; $R^2=0.35$, $n=19$. Overcast: $R_{\odot} = 165.28 \text{ W/m}^2 - 5.66T_a$; $R^2=0.20$, $n=24$. Suspended $T_b = 0.0099 R_{\odot} + 1.10 T_{a160 \text{ cm}} - 2.10^{\circ}$. Dorsal basking $T_b = 0.025 R_{\odot} + 1.18T_{a75 \text{ cm}} - 3.58^{\circ}$: R_{\odot} vs. T_a at start time on sunny days (Bitzer and Shaw, 1995).

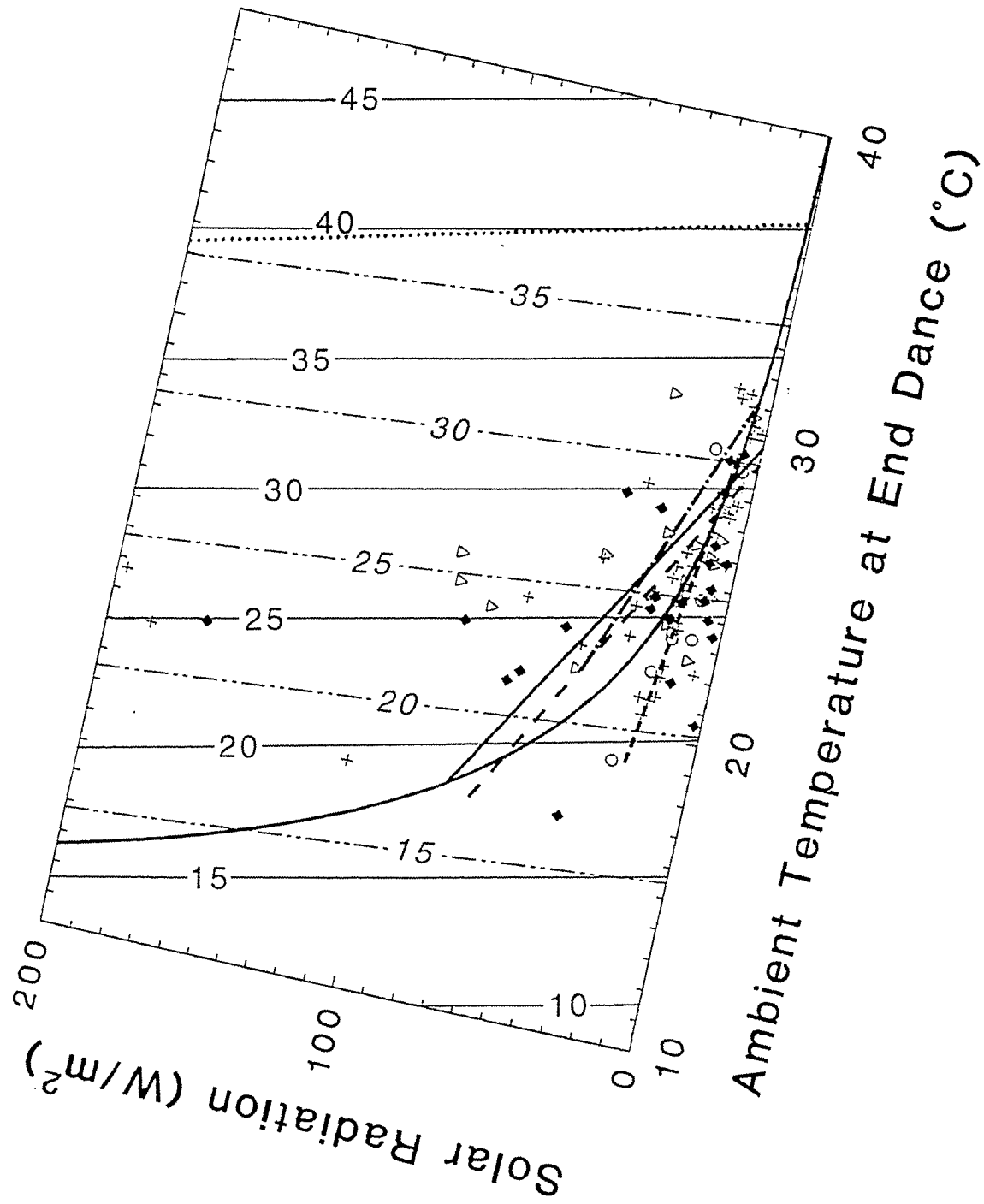


Table VI. End Dance Solar Radiation^a vs. Ambient Temperature, Cloud Cover, Wind Velocity, and Interaction Frequency.

Source	df	SS	<i>F</i>	<i>P</i>
Ambient temp. (T_a)	1	24993.21	25.68	<0.0001
Wind velocity (V_w)	1	5563.90	5.72	0.0190
Cloud cover	3	4834.09	1.66	0.1825
Interaction frequency (FREQ)	1	605.88	0.62	0.4322

^aEnd dance $R_{\odot} = 158.73 - 5.52T_a + 12.02V_w$. $R^2 = 0.29$, $F = 5.88$, $P < 0.0001$, $n = 94$, 6 treatment df.

no significant difference in the T_a - R_{\odot} relationship under different types of cloud cover, although T_a and R_{\odot} were highly correlated .

The T_a - R_{\odot} regression lines for the four sky conditions nonetheless cross suspended T_b isotherms from 18°C to 32°C (Fig. 7), suggesting that end dance occurred over a wide range of equilibrium body temperatures. The x-intercept of the regression line for sunny days, 29.8°C with $R_{\odot}=0$, estimates minimum T_b needed for *V. atalanta* males to fly. Even on sunny days there was much variance in end dance time ($R^2=0.26$, $F=13.91$, $P<0.0006$, $n=41$). The best-fitting exponential curve for sunny days (Fig. 7) parallels the T_b isotherms when T_a is low, but levels off at higher T_a .

When wind velocity (V_w) is higher, vagrant *V. atalanta* males stop flying earlier when solar radiation levels are higher. However, this relationship holds only on overcast days (from multiple regression by cloud cover, Table VII). There was no correlation of FREQ with variation in the T_a - R_{\odot} relationship (Tables VI, VII), nor was FREQ correlated with V_w ($r=-0.14$, $P=0.18$).

DISCUSSION

Excluding seasonal effects, the time of the last *V. atalanta* territorial interaction, or end dance, is correlated primarily with ambient temperature and secondarily with interaction frequency. To fly, locate mates, defend territories, etc., butterflies must obtain heat from the environment. The sun provides this energy by heating the air through which they fly, warming the substrate on which they perch, and warming their bodies directly. Air temperature is the most important of these heat sources in determining territorial end dance time. As T_a increases, end dance gets later, presumably because less heat is needed

Table VII. End Dance Solar Radiation^a vs. Ambient Temperature, Wind Velocity, and Interaction Frequency on Overcast Days ($n=24$).

Source	df	SS	F	P
Ambient temp. (T_a)	1	6416.07	6.66	0.0179
Wind velocity (V_w)	1	5745.52	5.96	0.0240
Interaction frequency (FREQ)	1	134.06	0.14	0.7131

^aEnd dance $R_{\odot} = 152.98 - 6.55T_a + 23.67V_w$. $R^2 = 0.38$, $F = 4.16$, $P < 0.0192$, $n = 24$, 3 treatment df.

from R_{\odot} . The sun's altitude is lower later in the day and less radiational heat is available. As with start time (Bitzer and Shaw, 1995), end dance times are earlier in spring and late summer than in mid-summer because the sun then reaches a particular altitude earlier in the afternoon.

The respective T_a coefficients show that end dance time varies by only ca. two-thirds as much per °C of T_a as does start time. End dance time = $14\text{h}.25 + 0.087T_a + 0.078\delta + 2.58\epsilon$, whereas start time = $11\text{h}.35 + 0.13T_a + 0.060\delta + 3.26\epsilon$ (Bitzer and Shaw, 1995). The variance of end dance time is also greater than that of the comparable start time model ($R^2=0.68$, $F=159.12$, $P<0.0001$, $n=224$, Bitzer and Shaw, 1995).

Interrelationship of Ambient Temperature, Solar Radiation, Wind Velocity, and Interaction Frequency Effects

V. atalanta males, like non-territorial *A. paphia* (Vielmetter, 1958), may utilize R_{\odot} and T_a to determine when to switch from flying to basking. Nevertheless, the regression line showing mean T_a and R_{\odot} at end dance time on sunny days (Fig. 7) spans a broad range of the T_b values measured for both dorsally-basking and suspended dead *V. atalanta* males. This contrasts with *V. atalanta* start time which occurs when T_b drops to a narrow range of levels (Fig. 7; also see Bitzer and Shaw, 1995). Since low light intensity (diffuse R_{\odot}) levels near dusk inhibit butterfly activity, even if T_a is favorable (Douwes, 1976; Saunders, 1982; Rawlins and Lederhouse, 1978; Dennis, 1993, p. 31), *V. atalanta* males may stop flying isothermally at low T_a , but be increasingly limited by oncoming darkness when the end dance occurs nearer sunset at higher T_a . The exponential curve depicted in Fig. 7 would then more accurately

represent the true T_a - R_{\odot} relationship for end dance. One cannot necessarily assume that seemingly linear T_a - R_{\odot} equations indicate an isotherm for equilibrium T_b , especially if they occur near dawn or dusk when solar radiation decreases non-linearly with solar altitude. The critical R_{\odot} at end dance time decreases much less rapidly per °C of T_a than does the critical start time R_{\odot} , a difference which may be partly due to flying butterflies being less responsive to R_{\odot} than dorsally basking butterflies. T_b of dorsal baskers = $0.034R_{\odot} + 1.19T_a - 3^{\circ}.42$ (unpublished data), whereas T_b of suspended butterflies = $0.0099R_{\odot} + 1.10T_{a160\text{ cm}} - 2^{\circ}.10$. These R_{\odot} coefficients indicate that suspended butterflies warm up by only one-third as much in sunshine as do dorsally basking ones, even though both warm up similarly as T_a increases.

R_{\odot} levels are much lower at end dance time than at start time. $R_{\odot} = 184.07\text{ W/m}^2 - 6.18T_a$ at end dance time on sunny days, whereas at start time, $R_{\odot} = 1557.46\text{ W/m}^2 - 41.94T_a$. Since *V. atalanta* males maintain a similar T_a - R_{\odot} relationship for end dance on overcast as well as sunny days (Fig. 7), end dance, unlike start time (Bitzer and Shaw, 1995), seems to be largely a response to radiational heat as Vielmetter (1958) found for *A. paphia*. Because similar R_{\odot} levels occur earlier on overcast than on clear afternoons, vagrant *V. atalanta* males stop flying correspondingly earlier on overcast days. This difference is greater when T_a is lower (Fig. 2). If the suspended T_b probes accurately represent actual T_b of flying intruders (see Rutowski, *et al.*, 1994), *V. atalanta* males should stop flying when their actual body temperatures drop below the critical level of 29.8°C, whatever the sky conditions. This value is lower than the 32°C minimum for vigorous flight which Heinrich (1986) indicates. We have

observed that the last few intruders' flight just before end dance tends to be weaker and more fluttery on some days.

End dance time probably indicates, at least in part, a climatic threshold below which non-territorial (vagrant) males can no longer fly between territories. Timing of end dance probably depends upon the lower body temperature of male intruders, which may go to roost before territorial males. *V. atalanta* occupants often patrol within their territories after end dance, suggesting they benefit from more protected conditions near the ground. Alcock (1985) suggested that male *Vanessa* butterflies perching on the ground maintain optimal body temperatures at a lower metabolic cost than by patrolling. We have likewise found (Bitzer and Shaw, unpublished data) that both open and closed freshly-killed *V. cardui* placed on the ground stay warmer throughout the territorial period than do dead *V. cardui* suspended at flight level (1.60 m), because they gain heat from the substrate and are protected from wind. *Why* occupants should stay in their territories for some time after the last flying butterflies have departed is a strategic question we consider when we examine end time itself (Bitzer and Shaw, in preparation).

Since vagrants' tendency to stop flying earlier under overcast seems to depend on climatic factors in the same way as on sunny days, a circadian rhythm modulated by T_a and possibly other climatic factors (see Bitzer and Shaw, 1995) is not needed to explain end dance timing, but cannot be ruled out by these data. The much greater difference between end dance under overcast vs. clear sky (Fig. 2) on cooler days indicates that *V. atalanta* males then depend upon R_{\odot} much more than they do on warmer days.

The Effects of Wind Around End Dance Time

A wind velocity effect upon end dance time is also likely. The analysis which included R_{\odot} and V_w suggests that vagrant *V. atalanta* males stopped flying earlier on windier days. Minimum R_{\odot} levels for flight are also higher on windier days (Tables VI, VII). Since *V. atalanta* males often flew steadily toward territories from considerable distances just before perching, they probably cool significantly more in flight on windy days and should thus stop flying earlier. We thus expected V_w to affect end dance time more strongly than it did start time (Bitzer and Shaw, 1995).

Vielmetter (1958) found no significant wind effect upon the T_a - R_{\odot} relationship for perching *A. paphia* due to low variability in V_w from day to day and a lack of calm days for comparison. Even though we found that V_w varied from calm to gusts of 20 m/s, with 1-min averages varying from 0-6 m/s, we found that V_w was not correlated with start time (Bitzer and Shaw, 1995). Perched *V. atalanta* males are well-protected from wind (Bitzer and Shaw, 1995). V_w is generally much lower near the ground (Campbell, 1977, pp.37-40); the effect of V_w (measured at 1.72 m where intruders fly) on T_s was small to insignificant (unpublished data).

Possible Interpopulation Variation of End Dance Time

Since *V. atalanta* males in some other parts of the U.S.A. (Shields, 1967, Swanson and Bitzer, in preparation) do not react to T_a and R_{\odot} at start time in the same way as does the population in Ames, Iowa (Bitzer and Shaw, 1995), we also expect the end dance schedule to differ between *V. atalanta* populations. Observations from other regions are needed to test this hypothesis. Differences

between start time solar altitude preferences suggest considerable genetic diversity in a migratory, cosmopolitan (Opler and Krizek, 1984; Larsen, 1993) butterfly population (Bitzer and Shaw, 1995). Yearly variation in both start time (Bitzer and Shaw, 1995) and end dance schedules could be due partly to migration of genetically distinct *V. atalanta* populations from different regions each year. However, yearly differences in end dance time do not necessarily parallel yearly start time differences, as might be expected if preferred T_b of different populations consistently varied. For example, both start times and end dance times were earlier than average in 1989, whereas in 1990, start times ran early and end dance times ran late. If, butterflies had been, say, less hirsute or smaller-bodied during 1989, they would have lost heat more rapidly, and consequently might have both perched and stopped flying at consistently earlier times in the afternoon. But such a hypothesis would not explain 1990 data.

End Dance Time, Interaction Frequency, Daily Schedule and Territorial Behavior

Although *V. atalanta* intruders stop flying at highly predictable times each day under most types of weather, climatic factors are only part of the story. End dance time becomes later as both FREQ and MAX increase, suggesting *V. atalanta*'s end dance time depends upon population density as well as climate. This contrasts with the highly climate-dependent start time (Bitzer and Shaw, 1995). If the last interaction does occur later on days when more males are flying, Iwasa and Obara's (1989) model is called into question for *V. atalanta* activity. Temporal distribution of *V. atalanta* males may instead be a "spillover" effect in which more males remain active later in the day simply because the peak male density was also higher. MAX may likewise increase as it becomes

more difficult at higher FREQ for an occupant to drive off one intruder before yet another alights in the territory unseen (Bitzer and Shaw, 1979). Perhaps on days when vagrant activity is higher, smaller males which cannot compete as effectively as larger ones (Bitzer and Shaw, in preparation) may arrive later in the territorial period when their chances of being driven off by another butterfly are lower.

Alcock and O'Neill (1986), to the contrary, found that *Strymon melinus* ceased spiral chasing earlier in the afternoon when several occupants or 10 or more vagrants swirled around a perch tree. This only occurred, however, when more than seven males were present. We never observed more than four joint *V. atalanta* occupants in a single territory during this study, a density probably too low to cause territorial breakdown.

Daily interaction frequency increases at higher T_a on cloudy days. This is consistent with Wickman and Wiklund's (1983) findings that more and more *Pararge aegeria* males switch to the patrolling strategy as T_a rises. Unlike *P. aegeria*, however, *V. atalanta* never abandoned territorial behavior completely at the highest T_a levels on any days. On sunny days, vagrant and interaction frequency peaks when T_a at end dance is ca. 27°C, and drops off under higher T_a . This finding suggests one of two possibilities. The first is that territories do increase in value at high as well as low T_a , inducing more males to perch at both temperature extremes (see Wickman and Wiklund, 1983). Since *V. atalanta* territories provide shade as well as sunshine, both sexes may value them as retreats from both extremes of T_a . The other possibility is that territories still become less valuable at high T_a , even though FREQ is also lower. If *V. atalanta* males do patrol for mates earlier in the day, FREQ could be low because more

vagrants have already mated on warmer days (Iwasa and Obara, 1989) and thus have less reason to enter and usurp territories later on.

The end dance schedule may be more density-dependent than start time because more opportunities exist later in the territorial period for complex feedback between weather and population density. For example, earlier end dance at lower densities might result when all the vagrants in an area have landed in previously unoccupied territories, while end dance may be later if there are many more males than territories. Meanwhile, more males might be vagrant on warmer days, both because they can fly later in the evening and because territories may then be less valuable. Yet we cannot draw the inverse conclusion that variations in population density are the only factor which causes end dance time or end time to be more variable than start time. Although *Argynnis paphia* is a non-territorial species, the transition event corresponding to end time is likewise more variant ($R^2=0.67$) than is the event corresponding to start time ($R^2=0.81$) (Vielmetter, 1958).

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CHAPTER 3. TERRITORIAL BEHAVIOR OF THE RED ADMIRAL,
Vanessa atalanta (LEPIDOPTERA: NYMPHALIDAE):
 III. THE ROLE OF CLIMATIC FACTORS, INTERACTION FREQUENCY,
 AND TIME OF LAST INTERACTION ON TERRITORIAL END TIME

A paper to be submitted to the Journal of Insect Behavior

Royce J. Bitzer^{1,2} and Kenneth C. Shaw¹

ABSTRACT

We examined the relative importance of climatic factors, population density, and time of the last interaction (end dance) to departure or end time of territorial *Vanessa atalanta* males. End time varies with solar altitude, which determines radiation (R_{\odot}) levels, and therefore varies seasonally. We removed seasonal effects by converting end times to corresponding solar altitudes. End time solar altitude (ETSA) correlates primarily with end dance solar altitude (EDSA) and ambient temperature (T_a) and secondarily with cloud cover and interaction frequency (FREQ). Overcast cloud cover resulted in earlier end times than under clear skies, as expected from reduced solar radiation levels which were similar at end times on both sunny and overcast days. Higher wind velocities (V_w) correlated with earlier end times and with correspondingly higher R_{\odot} levels at end time. Any possible perch substrate temperature (T_s) effects remained confounded with T_a . Waiting times after end dance (end time - end

¹Graduate student and Associate Professor, respectively,
 Department of Zoology and Genetics, Iowa State University.

²Author for correspondence.

dance time) on non-overcast days were similar (22.9 ± 13.7 min) over a wide range of T_a and FREQ. On overcast days, *V. atalanta* occupants waited longer to leave after end dance when FREQ was lower. We suggest that correlation of ETSA with climatic factors may result mainly from occupants waiting for a fixed time interval after end dance, itself correlated with climatic factors. There is no reason to believe that *V. atalanta* occupants choose to wait longer in their territories when FREQ, and presumably population density and the number of flying receptive females, are higher.

INTRODUCTION

Thermoregulatory strategies of butterflies are often combined opportunistically with mate location (Douwes, 1976; Shreeve, 1984; Dennis and Shreeve, 1988; Rutowski *et al.*, 1994; Bitzer and Shaw, 1995), and mating strategy in some species changes as both climatic and biological factors vary (Wickman and Wiklund, 1983; Wickman, 1985a; 1985b; 1988; Rutowski, 1991). If climatic factors are predictable over the course of the day, then so might be the period when butterflies perch or defend territories. We have examined the relative importance of climatic factors and interaction frequency to the territorial start time (Bitzer and Shaw, 1995) and end dance time (Bitzer and Shaw, in preparation) of *Vanessa atalanta*. Start time is highly correlated with climatic factors, most notably ambient temperature (T_a), but not with early interaction frequency, whereas end dance time is correlated with both T_a and interaction frequency (FREQ).

Vielmetter (1958) found that ambient temperature (T_a) and solar radiation (R_{\odot}) interacted inversely to cause the non-territorial nymphalid butterfly

Argynnis paphia to switch between continuous flight and stationary basking at a critical body temperature (T_b) of 34.2°C. A similar relationship was found for *V. atalanta* start time on sunny days (Bitzer and Shaw, 1995). *A. paphia* decamps from its perch at a lower critical T_b of 23.4°C and flies up into nearby trees (*Baumflug*) to roost (Vielmetter, 1958). Douwes (1976) found similar activity patterns for *Heodes virgaureae*.

When T_a is low, there seems to be an intermediate critical T_b at which *V. atalanta* males can fly within but not between territories. When the environment cools to this point, intruders cease entering occupied territories and any subsequent territorial interactions occur between joint occupants. Vagrant males seem to be limited by oncoming darkness rather than T_b at higher T_a levels. The time when this occurs can be estimated from the final territorial interaction of the day, the *end dance* (Bitzer and Shaw, in preparation). End time may likewise be limited partly by low light levels.

As do start time (Swanson, 1979; Swanson and Bitzer, in preparation; Bitzer and Shaw, 1995) and end dance time (Bitzer and Shaw, in preparation), end time should vary with solar declination, with the latest times occurring toward mid-summer. Brown and Alcock (1991) have likewise shown that arrival and departure times of *Vanessa* sp. vary with solar declination.

We also examined the relationship between start and end dance time and secondary climatic factors as cloud cover, wind velocity and direction, and substrate temperature (Bitzer and Shaw, 1995; in preparation). Do these factors affect or are they related to end time in similar ways? *V. atalanta* males respond to solid overcast by perching later than they do on clear days, rather than earlier as one would expect from the corresponding solar radiation levels

(Bitzer and Shaw, 1995). This behavior might result from lower substrate temperature (T_s) on overcast days (Bitzer and Shaw, 1995), or because males benefit somehow from patrolling later under overcast (Bitzer and Shaw, 1995, Dennis and Williams, 1987). In contrast, end dance occurs when R_{\odot} drops below a T_a -dependent critical level, regardless of cloud cover. The last territorial interaction thus occurs earlier on overcast than on clear days. How, then, does cloud cover affect end time? We also expect substrate temperature to be important to perched occupants. Since *V. atalanta* males decamp from perches on the ground, we expect that as with start time (Bitzer and Shaw, 1995), end time may be correlated with substrate temperature but not with wind velocity.

Population density of conspecific males as well as climatic factors may affect butterflies' activity schedules. End dance time gets later as both T_a and FREQ increase (Bitzer and Shaw, in preparation). The latter finding is contrary to predictions using Iwasa and Obara's (1989) game theory model that end dance should occur earlier on days when more males are active (Bitzer and Shaw, in preparation). If *V. atalanta* males wait for a relatively constant time interval after end dance to leave their territories, end time might depend indirectly upon the climatic population density factors affecting end dance. This possibility, however, does not rule out an accompanying direct effect of climatic factors upon end time.

As with start time, interspecific interactions between sympatric species (Bitzer and Shaw, 1983, Gaugler and Schutz, 1989), or need to avoid periods when predators are active, could also affect when both perched and vagrant males fly. Intruders and decamping occupants may be vulnerable to birds, bats

and other aerial predators, whereas perched occupants may be vulnerable to chameleons (Swanson, 1979) or similar ground-dwelling predators.

We identify correlations of several climatic and population density variables with territorial end time and determine their relative importance. We also present evidence that the time when each occupant decamps from its territory to seek a roost is more predictable from the end dance time than it is from T_a and other climatic variables. We believe that correlations of climatic variables with end time may be mainly an artifact of their correlation with end dance, which then directly affects end time. On this basis we develop a model to which end time of other populations or species might be compared. These findings pose questions for future experimental work on end time.

MATERIALS AND METHODS

Butterflies were observed on the Iowa State University campus between April and September from 1987-1992. We recorded a total of 204 end times. These were defined as the time when the occupant flew up from his territory and failed to return. Departure flights were distinct from patrols because the occupant abruptly rose from his perch at a ca. 50-60° angle until reaching the upper branches of surrounding trees, and then sought a roost site. We analyzed data from 198 end times for which we had complete information on ambient temperature (T_a), end dance (last interaction with an intruder), interaction frequency (FREQ), and maximum number of joint occupants (MAX), including one primary and up to three secondary occupants. For the 94 end times recorded from 1989 to 1992, we also measured solar radiation (R_{\odot}), wind velocity (V_w), and substrate temperature (T_s). Two observations when no

intruders arrived (FREQ=0) were discarded from two analyses (n=196) using base-10 logarithms of FREQ. Both were from overcast days.

We observed end times at 10 optimal [most frequently occupied, (Bitzer and Shaw, 1979)] territorial sites on campus, most often at the two optimal sites (Territories 11 and 13) described in Bitzer and Shaw (1995). Sunlight fell in these areas most strongly before 1600 CST, then became increasingly patchier, and was gone by 1910-1930. End time was usually recorded in Territory 11 (123 of 198 obs.) and in Territory 13 (52 obs.). On 11 days, we recorded end times in both Territory 11 and Territory 13. We also recorded whether an occupant decamped while resting (141 obs.), or because it was disturbed by a pedestrian, (45 obs.) or if it decamped while interacting (1 obs.), patrolling (10 obs.), or chasing a bird (1 obs.), mainly to see whether or not butterflies left significantly earlier when disturbed.

We used both FREQ and MAX to estimate population density during the territorial period. We calculated FREQ by dividing the total number of intruders which interacted with occupants by the duration of the territorial period. For vagrant butterflies to become secondary occupants, they had to remain in the territory after one bout of interactions.

End time and end dance time were recorded to the nearest second (Central Standard Time) with a digital quartz clock/stopwatch set by time signals from the National Bureau of Standards (NBS) radio station WWV, and were converted to four-place decimal equivalents. Solar altitude corresponding to each end time and end dance time was calculated as in Campbell (1977, p. 53). Latitude (42°01'38"N) and longitude (93°38'42"W) of the territorial sites were taken from a USGS topographical map. Solar declination (angular distance of

the sun north or south of the equator) and ephemeris time of solar noon were taken from the *Astronomical Almanac* (1987-1992). Time of solar noon was corrected for longitude. Solar altitude values were uncorrected for atmospheric refraction.

Ambient temperature (T_a), cloud cover, and wind velocity (V_w) were recorded from 1987 through 1992 as in Bitzer and Shaw (1995). Substrate temperature (T_s) was recorded in ground-based territories on 94 days from 1989 through 1992 as in Bitzer and Shaw (1995). We also used an Everest Interscience, Inc. Model 120 handheld infrared thermometer during 1991 and 1992 to read T_s of perch sites in both territories. These readings varied no more than 0.3°C from thermocouple readings of the same spots. Emissivity of soil and stone was assumed to be 0.95; that of vegetation, 0.98, in accord with standard practice (see Monteith and Unsworth, 1990, pp. 81-85).

We estimated equilibrium body temperature (T_b) of dorsally-basking butterflies from 1989 through 1992 as in Bitzer and Shaw (1995) and of closed perched butterflies during 1992. The T_b and T_s probes were kept with the pyranometer within a 60-cm circle under similar levels of solar radiation, with no probes shading any others.

Multiple regression and analysis of covariance (ANCOVA) were used to analyze statistical models unless one or more of the independent variables were correlated with each other. If so, we used principal components analysis to identify both distinct groups of continuous variables and linear combinations of the original variables which had the smallest variance. Principal components derived from these variables were then analyzed in ANCOVA models containing the discrete variables of departure mode, year, territory site, and cloud cover.

Simple correlations were used to examine and graph relationships between end time and each of the independent variables.

RESULTS

Analyses Excluding End Dance

End Time Varies with Ambient Temperature, Time of Year, and Interaction Frequency

End time was correlated with T_a , occurring later when T_a was higher (Fig. 1, $R^2=0.38$, $F=122.22$, $P<0.0001$, $n=198$). End time increased linearly by 7.89 min for each additional 1°C of T_a .

Occupants decamped 20-60 min earlier at the same T_a in early May and in August through September than they did from mid-May through July (Fig. 1). Seasonal changes in both solar declination (δ) and time of solar noon (ϵ) correlated with end time (Table I). End times for any particular T_a were earlier when δ was lower, and also followed seasonal variations in ϵ . Accounting for both δ and ϵ explained an additional 20% of the residual variability in the first model ($R^2=0.58$, $F=89.38$, $P<0.0001$, $n=198$).

Interaction frequency (Table I) was weakly correlated with end time, as compared with the above factors and cloud cover. End time was 0.30 min (18 s) later per unit increase in interaction frequency. This compares with +5.64 min/ $^\circ\text{C}$ and +5.34 min/degree of solar declination in the full model.

When the relationship of end time to T_a was partitioned by cloud cover (Fig. 2), we found that end time changed more rapidly with T_a under cumuloform clouds and overcast than under clear skies and cirroform clouds.

Figure 1. Relationship of ambient temperature (T_a) and solar declination (δ) to end time (hours CST). Sky conditions: + : Clear sky; O: Cirroform cloudiness; ∇ : Cumuliform cloudiness; \blacklozenge : Overcast.

———— : Regression line for all 198 observations (End time = $15\text{h}.92 + 0.13 T_a$).

- - - - - : End time line for 21 June ($\delta = +23^\circ.4433$). - - - - - : Line for 21 April/August ($\delta = +12^\circ$). To simplify the graph, time of solar noon was set at 12h 17 min 03s (12h.2841), near the mean value for all data; thus $\epsilon = 17 \text{ min } 03\text{s}$ (0h.2841). End time = $14\text{h}.11 + 0.10T_a + 0.090\delta + 2.54\epsilon$: Start time vs. T_a from Bitzer and Shaw (1995). Heavy dashed line: End dance time vs. T_a from Bitzer and Shaw (in preparation).

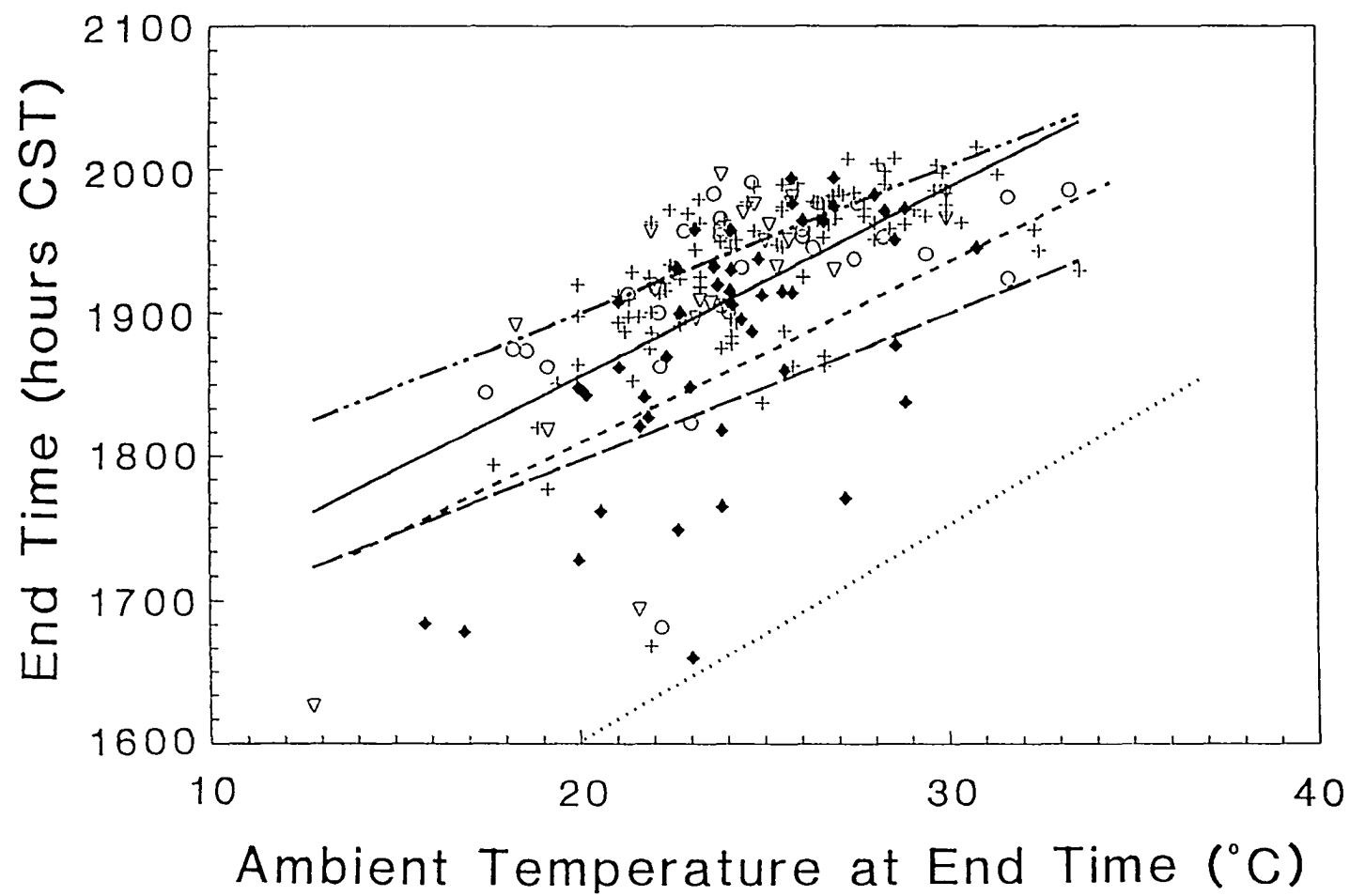


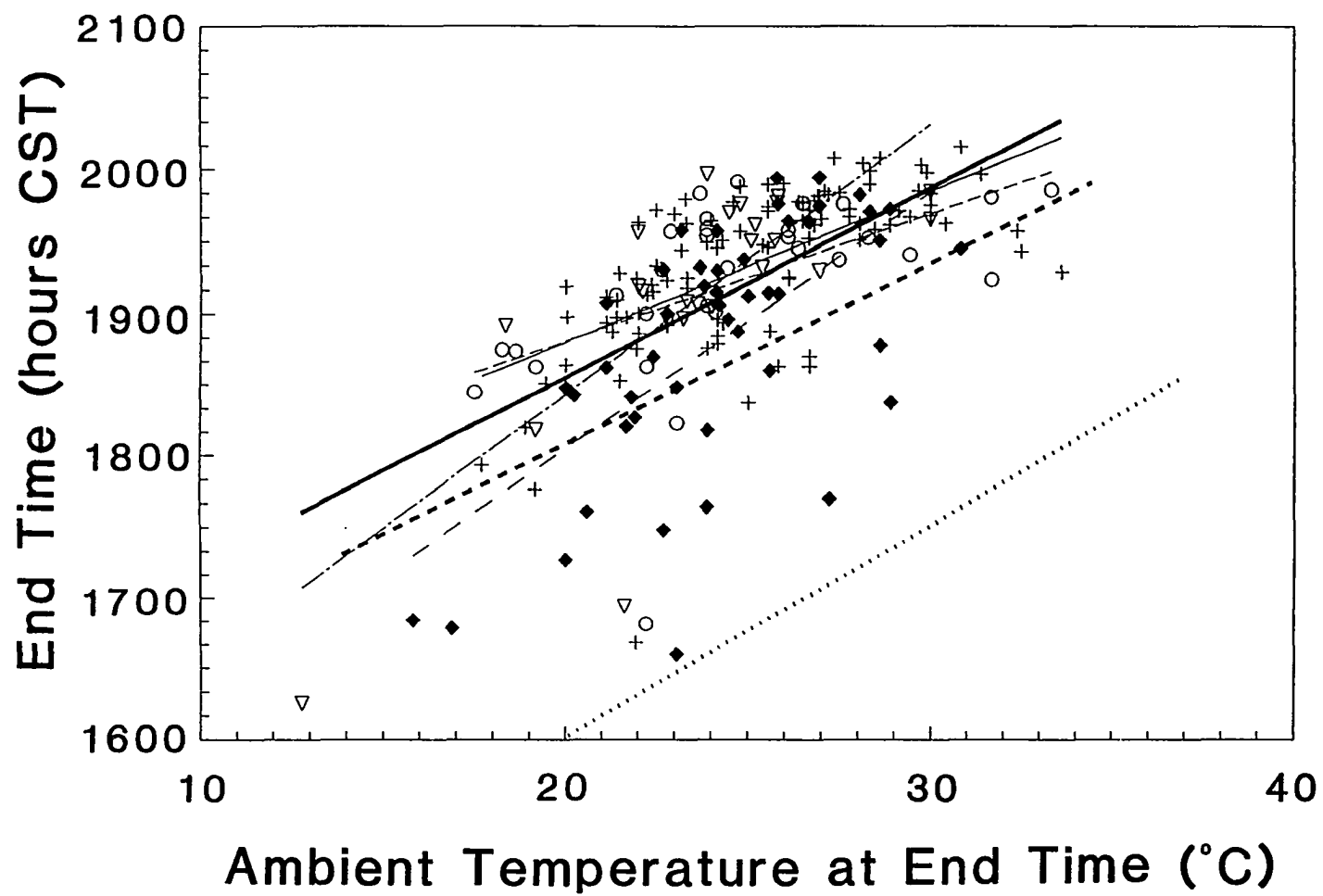
Table I. End Time^a vs. Ambient Temperature (T_a), Solar Declination (δ), Transit Variation from Solar Noon (ϵ), Interaction Frequency, and Cloud Cover.

Source	df	SS	F	P
Ambient temp. (T_a)	1	17.23	88.06	<0.0001
Declination (δ)	1	16.72	85.45	<0.0001
Solar noon variation (ϵ)	1	3.90	19.94	<0.0001
Interaction frequency (FREQ)	1	0.81	4.16	0.0428
Cloud cover	3	5.49	9.35	<0.0001

Cloud cover	Adjusted mean ETSA	C. cover difference	Different from clear? t	P
Overcast	18h.87	-0h.41	-5.15	<0.0001
Cumuliform	19h.16	-0h.12	-1.18	0.2405
Cirroform	19h.25	-0h.03	-0.39	0.6975
Clear	19h.29	0	-	-

^aEnd time = $14\text{h.}40 + 0.094 T_a + 0.089 \delta + 2.54 \epsilon + 0.005 (\text{FREQ}) + \text{Cloud cover difference}$. $R^2 = 0.65$, $F = 49.66$, $P < 0.0001$, $n = 198$, 7 treatment df.

Figure 2. Relationship of ambient temperature (T_a) to end time (hours CST), by cloud cover. Sky conditions are indicated as in Fig. 1. — : Regression line for all 198 observations (End time = $15\text{h}.92 + 0.13 T_a$). — : End time line for clear skies (End time = $16\text{h}.71 + 0.10T_a$, $R^2=0.39$, $F=60.47$, $P<0.0001$, $n=97$). - - - - - : Cirroform cloudiness ($17\text{h}.04 + 0.09T_a$, $R^2=0.29$, $F=11.31$, $P=0.0022$, $n=30$). - . - . - . : Cumuliform cloudiness ($14\text{h}.67 + 0.19T_a$, $R^2=0.54$, $F=30.89$, $P<0.0001$, $n=24$). - - - - - : Overcast ($14\text{h}.46 + 0.18T_a$, $R^2=0.41$, $n=47$). : Start time vs. T_a from Bitzer and Shaw (1995). Heavy dashed line: End dance time vs. T_a from Bitzer and Shaw (in preparation).

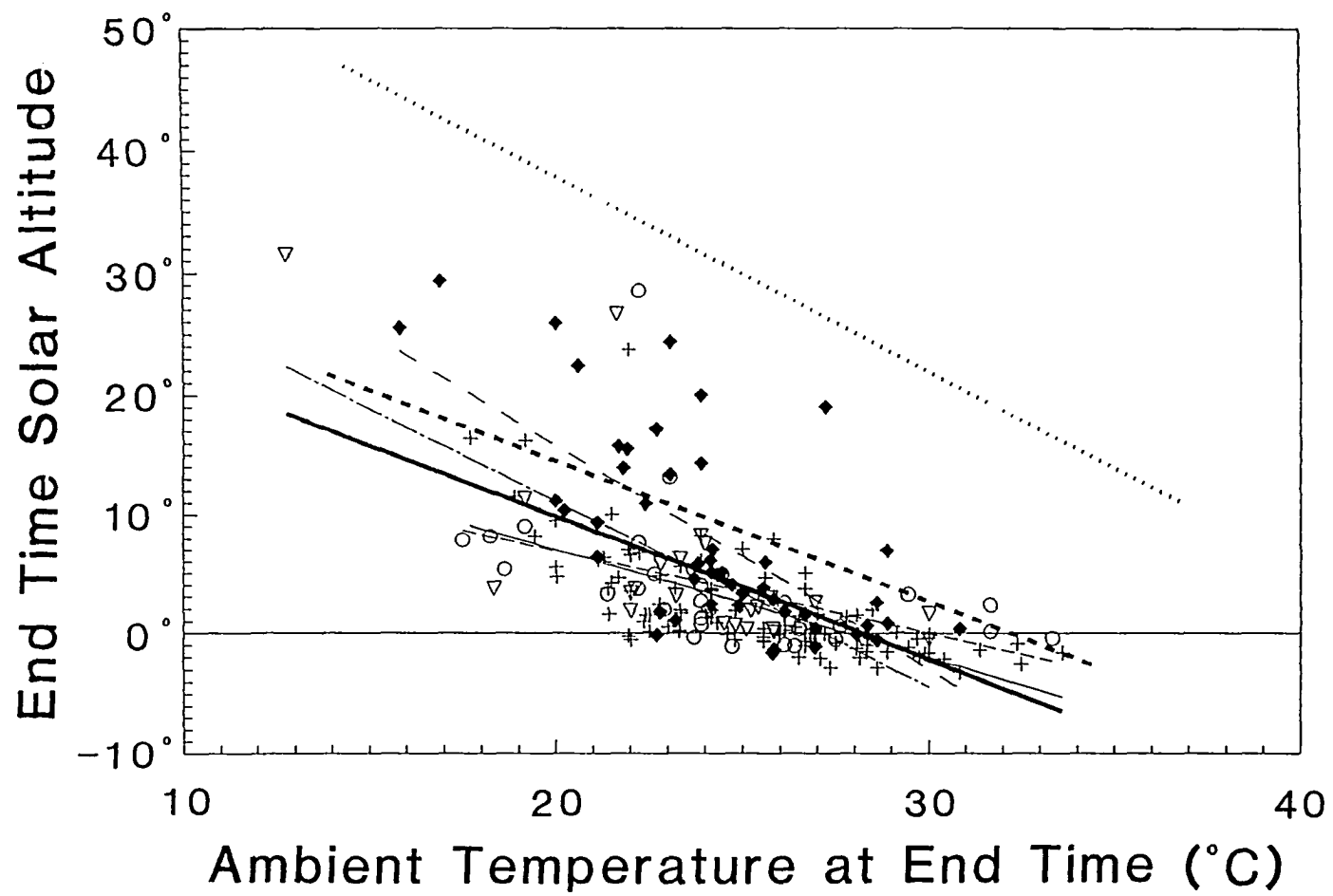


The difference in end time between clear and overcast days was greater when T_a was lower (Fig. 2).

Similar effects of cloud cover appeared when end time was expressed as the corresponding solar altitude. Regressing the end time solar altitude (ETSA) against T_a (Fig. 3) combined end time, δ , and ϵ into a single factor, yielding a model ($R^2=0.39$, $F=125.16$, $P<0.0001$, $n=198$) analogous to Vielmetter's (1958) analysis of *Baumflug*. The sun averaged $1^\circ.20$ lower (ca. 6.68 min later) at end time for each increase of 1°C . As shown by the higher R^2 values, end time was more predictable for sunny days ($R^2=0.47$, $F=83.34$, $P<0.0001$, $n=97$), overcast days ($R^2=0.48$, $F=42.03$, $P<0.0001$, $n=47$), and cumuliform-clouded days ($R^2=0.50$, $F=22.05$, $P<0.0001$, $n=24$) than it was for all sky conditions combined. There was no significant difference between clear and cirroform days ($t= -0.39$, $P=0.70$), between cirroform and cumuliform days ($t= -0.68$, $P=0.50$), or between clear and cumuliform days ($t= -1.18$, $P=0.24$). Nevertheless, it seemed that the slopes for the thicker cloud types were similar to each other and different from those for cirroform clouds and clear sky.

V. atalanta males on sunny days fly off to roost based on an inverse relationship between T_a and solar altitude, the latter determining the amount of solar radiation (Vielmetter, 1958). Solar radiation (R_\odot) on clear afternoons decreases linearly with solar altitude, except near sunset when the sun is less than 10° up (Campbell, 1977, p. 56). Plotting end time of territorial butterflies as a solar altitude value allows one to compare activity schedules of different populations and different species located in various latitudes.

Figure 3. Relationship of ambient temperature (T_a) to end time (expressed as the corresponding solar altitude). Sky conditions are indicated as in Fig. 1. — : Regression line for all 198 observations ($ETSA = 33^\circ.84 - 1.20T_a$). — : Clear sky: $ETSA = 24^\circ.98 - 0.90T_a$, $R^2=0.47$, $F=83.34$, $P<0.0001$, $n=97$. - - - - - : Cirroform cloudiness: $ETSA = 20^\circ.79 - 0.69T_a$, $R^2=0.21$, $F=7.56$, $P=0.0103$, $n=30$. - . - . - . : Cumuliform cloudiness: $ETSA = 42^\circ.17 - 1.55T_a$, $R^2=0.50$, $F=22.05$, $P<0.0001$, $n=24$. - - - - - : Overcast: $ETSA = 53^\circ.37 - 1.87T_a$, $R^2=0.48$, $F=42.03$, $P<0.0001$, $n=47$: Start time solar altitude vs. T_a from Bitzer and Shaw (1995). Heavy dashed line: end dance solar altitude from Bitzer and Shaw (in preparation).



Analyses Including End Dance

*Principal Components Analysis of Ambient Temperature,
End Dance Solar Altitude, Interaction Frequency,
and Maximum Number of Simultaneous Occupants*

This model used all 198 observations from 1987-1992. Simple correlations of T_a , EDSA, FREQ, and MAX showed that T_a was correlated with EDSA ($r=-0.60$, $P<0.0001$, $n=198$) and FREQ ($r=0.16$, $P=0.0287$), but not with MAX ($r=0.12$, $P=0.0795$). EDSA was correlated with FREQ ($r=-0.33$, $P<0.0001$) and MAX ($r=-0.22$, $P=0.0017$), and FREQ was correlated with MAX ($r=0.44$, $P<0.0001$).

Principal components analysis showed that the eigenvalues of the first two principal components contained 76.8% of the total variance (Table II). Prin 4 contained 9.2% of the total variance, small enough to determine the relative importance of the four continuous variables (see Gaugler and Schutz, 1989). EDSA had the strongest effect upon end time, followed by T_a , FREQ, and MAX. The eigenvectors of the variables (Table III) indicate that EDSA effects lie primarily in Prin 1 and MAX effects mainly in Prin 2, whereas T_a and FREQ effects are distributed evenly between Prin 1 and Prin 2.

Prin 1 and Prin 2 were then analyzed in an ANCOVA along with the class variables of departure mode, year, territory site, and cloud cover (Table IV). Of all these, only variations in Prin 1, Prin 2, and departure mode correlated with EDSA. Departure mode, however, was significant only because end dance was earlier (EDSA was higher) for *V. atalanta* territory occupants which decamped during an interaction. Otherwise occupants flew off at similar times whether they were disturbed or undisturbed. Prin 1 being stronger than Prin 2 suggests that EDSA most strongly affects end time. Prin 2, however, was also highly

Table II. Principal Components Analysis of End Time. Continuous independent variables include ambient temperature, interaction frequency, and maximum number of joint occupants.

Principal component	Eigenvalue ^a	Proportion of variance ^b
1	1.954	0.489
2	1.118	0.279
3	0.562	0.140
4	0.366	0.092

^aEigenvalues represent variance of principal component.

^bProportion of total variance included in principal component.

Table III. Eigenvectors of Individual Variables for Principal Components 1, 2, and 4.

Principal component	1	2	4
Variable			
End dance solar altitude (EDSA)	-0.582	0.352	0.724
Ambient temperature (T_a)	0.502	-0.547	0.638
Interaction frequency (FREQ)	0.479	0.486	0.256
Maximum no. of occupants (MAX)	0.423	0.584	-0.052

Table IV. End Time Solar Altitude^a vs. Principal Components 1 and 2, Departure Mode, Year, Territory Site, and Cloud Cover.

Source	df	SS	<i>F</i>	<i>P</i>
Prin 1	1	3222.93	302.94	<0.0001
Prin 2	1	1058.07	99.45	<0.0001
Departure mode	4	163.23	3.84	0.0051
Year	5	103.21	1.94	0.0899
Territory site	7	85.37	1.15	0.3364
Cloud cover	3	54.44	1.71	0.1676

Departure mode	Adjusted mean ETSA	D. mode difference	Diff. than from perch? <i>t</i>	<i>P</i>
Bird chase	2°.34	-1°.47	-0.44	0.6603
Disturbed by pedestrian	3°.71	-0°.10	-0.17	0.8688
During an interaction	17°.35	13°.54	3.88	<0.0001
During a patrol	3°.66	-0°.15	-0.13	0.8991
From perch	3°.81	0	-	-

^aETSA = 3°.65 - 3.22(Prin 1) + 2.40(Prin 2) + Departure mode difference.

$R^2 = 0.78$, $F = 30.18$, $P < 0.0001$, $n = 198$, 21 treatment df.

Prin 1 = -0.58(EDSA - 8.14)/6.40 + 0.50(T_a - 24.71)/3.44 + 0.48(FREQ - 12.41)/13.11 + 0.42(MAX - 1.59)/0.68 (Mainly end dance solar altitude).

Prin 2 = 0.35(EDSA - 8.14)/6.40 - 0.55(T_a - 24.71)/3.44 + 0.49(FREQ - 12.41)/13.11 + 0.58(MAX - 1.59)/0.68 (Mainly ambient temperature).

significant, suggesting that even MAX could affect end time. T_a and FREQ effects contributed to both principal components (Table IV).

*Principal Components Analysis of End Dance Solar Altitude, Interaction
Frequency, Maximum Number of Simultaneous Occupants, Ambient
Temperature, Solar Radiation,
Substrate Temperature, and Wind Velocity*

This model used 94 observations from 1989-1992. Simple correlations of FREQ, MAX, T_a , R_{\odot} , T_s , and V_w showed correlations between FREQ and MAX ($r=0.43$, $P<0.0001$), FREQ and T_a ($r=0.27$, $P=0.0074$), MAX and T_a ($r=0.28$, $P=0.0072$), T_a and R_{\odot} ($r=-0.50$, $P<0.0001$), FREQ and T_s ($r=0.30$, $P=0.0031$), MAX and T_s ($r=0.25$, $P=0.0172$), T_s and R_{\odot} ($r=-0.37$, $P=0.0002$), T_a and T_s ($r=0.73$, $P<0.0001$) and R_{\odot} and V_w ($r=0.26$, $P=0.01$). EDSA was correlated with the other six variables as well, with P ranging from 0.0215 for V_w ($r=0.24$) to <0.0001 for T_a ($r=-0.54$). As was true of the preceding analysis, population density and T_a effects are confounded.

Principal components analysis showed that the eigenvalues of the first three principal components contained 75.8% of the total variance (Table V). Prin 7 contained only 2.6% of the total variance, and was thus used to determine relative importance of the six continuous variables as in Gaugler and Schutz (1989). The eigenvectors of the variables (Table VI) indicate that EDSA, T_a and T_s effects lie mainly in Prin 1, V_w effects lie mainly in Prin 2, while Prin 3 contains mainly R_{\odot} , FREQ, and MAX effects.

Prin 1, 2 and 3 were then analyzed in an ANCOVA along with the class variables of cloud cover, year, and territory site (Table VII). Prin 1 showed that EDSA varied with EDSA, T_a and T_s . Prin 2, strongly representing V_w , was insignificant. Prin 3 indicated that EDSA varied with both R_{\odot} and the

Table V. Principal Components Analysis of End Time. Continuous independent variables include ambient temperature, solar radiation, substrate temperature, wind velocity, interaction frequency, and maximum number of joint occupants.

Principal component	Eigenvalue ^a	Proportion of variance ^b
1	2.974	0.425
2	1.227	0.175
3	1.108	0.158
4	0.584	0.083
5	0.507	0.073
6	0.416	0.059
7	0.183	0.026

^aEigenvalues represent variance of principal component.

^bProportion of total variance included in principal component.

Table VI. Eigenvectors of Individual Variables for Principal Components 1, 2, 3, and 7.

Principal component	1	2	3	7
Variable				
End dance solar altitude (EDSA)	-0.466	0.167	0.049	0.160
Ambient temperature (T_a)	0.472	0.395	-0.186	0.764
Solar radiation (R_\odot)	-0.375	0.192	0.459	0.252
Substrate temperature (T_s)	0.456	0.244	-0.163	-0.478
Wind velocity (V_w)	-0.093	0.824	0.154	-0.309
Interaction frequency (FREQ)	0.343	-0.199	0.531	0.028
Maximum no. of occupants (MAX)	0.291	-0.007	0.648	-0.041

Table VII. End time solar altitude^a vs. principal components 1, 2, and 3, departure mode, cloud cover, territory site, and year.

Source	df	SS	<i>F</i>	<i>P</i>
Prin 1	1	1386.75	121.34	<0.0001
Prin 2	1	1.53	0.13	0.7156
Prin 3	1	95.55	8.36	0.0050
Departure mode	3	212.02	6.18	0.0008
Cloud cover	3	101.12	2.95	0.0379
Territory site	4	82.33	1.80	0.1372
Year	3	29.24	0.85	0.4693

Departure mode	Adjusted mean ETSA	D. Mode difference	Diff. than from perch? <i>t</i>	<i>P</i>
Disturbed by pedestrian	4°.42	-0°.75	-0.85	0.3996
During an interaction	19°.65	14°.48	3.87	0.0002
During a patrol	1°.48	-3°.68	-1.71	0.0920
From perch	5°.16	0	-	-

Cloud cover	Adjusted mean ETSA	C. cover difference	Different from clear? <i>t</i>	<i>P</i>
Overcast	9°.67	2°.57	2.51	0.0141
Cumuliform	7°.89	0°.80	0.79	0.4342
Cirroform	6°.06	-1°.03	-0.84	0.4057
Clear	7°.10	0	-	-

^aETSA = 4°.94 - 2.64(Prin 1) + 1.16(Prin 3) + Departure mode difference + Cloud cover difference. $R^2 = 0.76$, $F = 15.94$, $P < 0.0001$, $n = 94$, 16 treatment df.

Prin 1 = $-0.47(EDSA - 7.95)/6.25 + 0.47(T_a - 24.30)/3.02 - 0.38(R_{\odot} - 12.18)/25.18$
 $+ 0.46(T_s - 25.64)/3.32 - 0.09(V_w - 1.08)/0.68 + 0.34(FREQ - 11.50)/9.36$
 $+ 0.29(MAX - 1.46)/0.63$ (Mainly end dance solar altitude, ambient and
 substrate temperatures).

Prin 2 = $0.17(EDSA - 7.95)/6.25 + 0.40(T_a - 24.30)/3.02 + 0.19(R_{\odot} - 12.18)/25.18$
 $+ 0.24(T_s - 25.64)/3.32 + 0.82(V_w - 1.08)/0.68 - 0.20(FREQ - 11.50)/9.36$
 $+ 0.007(MAX - 1.46)/0.63$ (Mainly wind velocity).

Prin 3 = $0.05(EDSA - 7.95)/6.25 - 0.19(T_a - 24.30)/3.02 + 0.46(R_{\odot} - 12.18)/25.18$
 $- 0.16(T_s - 25.64)/3.32 + 0.15(V_w - 1.08)/0.68 + 0.53(FREQ - 11.50)/9.36$
 $+ 0.65(MAX - 1.46)/0.63$ (Mainly solar radiation and population density
 factors).

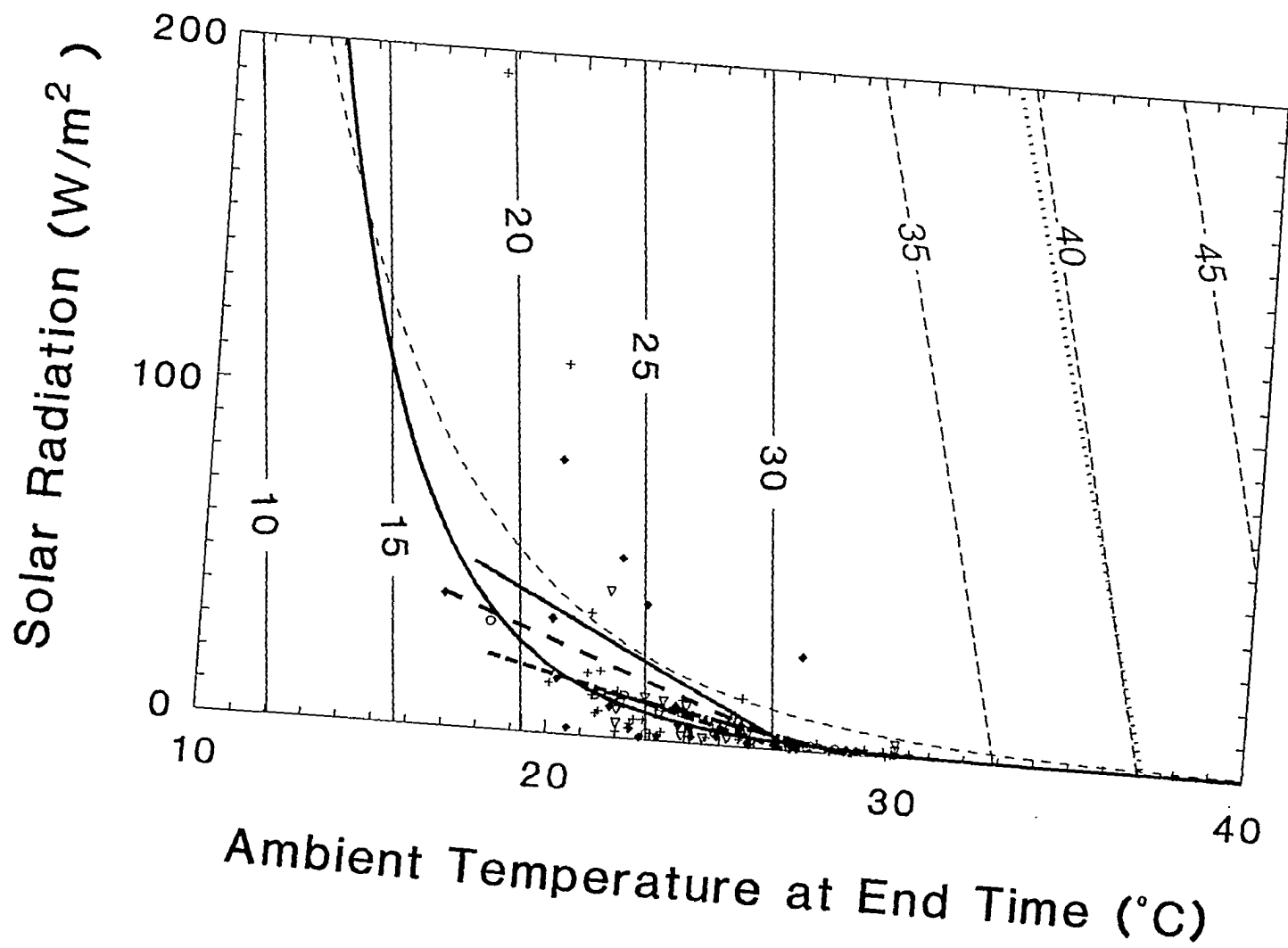
population density factors. Prin 7 indicates that T_a and T_s (Prin 1) are the strongest predictors of ETSA (end time was later when T_a was higher and T_s was lower, Table VI). EDSA, R_{\odot} and V_w (from Prin 1 and Prin 3) were weaker predictors (end time was later when EDSA was later, R_{\odot} was higher and V_w was lower), and FREQ and MAX (Prin 2) were not significant predictors of end time (ETSA) in this analysis. This result contradicts that of the previous analysis (Table IV) which found EDSA to be the factor most strongly correlated with end time.

Cloud cover appeared as significant in this analysis. ETSA was higher (end time was ca. 14.31 min earlier) for overcast compared with clear conditions (Table VII). ETSA's for either cumuliform or cirroform skies were not significantly different from those for clear skies, but were significantly different from those for overcast skies (cumuliform: $t=3.31$, $P=0.0014$; cirroform: $t=3.32$, $P=0.0014$).

*Relationship between Ambient Temperature, Solar Radiation
and Body Temperature at End Time*

Plotting R_{\odot} against T_a at end time (Fig. 4) showed that vagrant butterflies stop flying when R_{\odot} and T_a decline to critical levels, whatever the cloud cover. An ANCOVA model for the four sky conditions ($R^2=0.41$, $F=9.94$, $P<0.0001$, $n=94$) indicated no significant difference in the T_a - R_{\odot} relationship under different types of cloud cover ($F=1.37$, $P=0.26$), although T_a and R_{\odot} were highly correlated ($F=43.89$, $P<0.0001$). The regression line for overcast skies was similar to those for clear skies (no significant difference; $t=-1.58$, $P=0.12$) and cumuliform-clouded skies ($t=0.47$, $P=0.64$). Because R_{\odot} levels are similar earlier in the afternoon under overcast skies, perched *V. atalanta* males

Figure 4. Correlation of ambient temperature (T_a) and solar radiation (R_{\odot}) at end time on 94 days. Sky conditions and the corresponding regression lines are indicated as in Fig. 2. Sloping solid contour lines are isotherms of equilibrium body temperature (T_b) of freshly-killed *V. atalanta* males at rest on the ground with wings folded and parallel to the sunlight, recorded at 1-min intervals during the territorial period on 6 days in 1992 ($n = 577$). Dashed contour lines with italicized labels: isotherms ($^{\circ}\text{C}$) of equilibrium T_b of freshly-killed males in dorsal basking position, measured at 1-min intervals during the territorial period on 10 days in 1992 ($n=1013$). After locating T_a and R_{\odot} on the axes, read the predicted T_b from the diagonal isotherm contours. *V. atalanta* end time: Clear sky, linear: $R_{\odot} = 141.73 \text{ W/m}^2 - 5.20T_a$; $R^2=0.26$, $F=13.93$, $P=0.0006$, $n=41$. Clear sky, exponential: $R_{\odot} = 14,817.9e^{-0.329T_a}$; $R^2=0.65$. Cirroform cloudiness: $R_{\odot} = 70.25 \text{ W/m}^2 - 2.59T_a$; $R^2=0.70$, $F=19.03$, $P=0.0024$, $n=10$. Cumuliform cloudiness: $R_{\odot} = 54.27 \text{ W/m}^2 - 1.88T_a$; $R^2=0.23$, $F=5.17$, $P=0.0362$, $n=19$. Overcast: $R_{\odot} = 105.01 \text{ W/m}^2 - 3.82T_a$; $R^2=0.27$, $F=8.26$, $P=0.0088$, $n=24$. T_b with closed wings = $0.0096 R_{\odot} + 1.38 T_{a75 \text{ cm}} - 6.55^{\circ}$. Dorsal basking $T_b = 0.025 R_{\odot} + 1.18T_{a75 \text{ cm}} - 3.58^{\circ}$: R_{\odot} vs. T_a at start time on sunny days (Bitzer and Shaw, 1995). - - - - - : exponential estimate of end dance time from Bitzer and Shaw (in preparation).



consequently decamp earlier on overcast days than on clear days. This difference is more pronounced when T_a is low (Fig. 2).

The T_a - R_{\odot} regression lines for the four sky conditions nonetheless cross T_b isotherms from 17°C to 29°C (Fig. 4), suggesting that end time occurred over a wide range of equilibrium T_b . The x-intercept of the regression line for sunny days, 27.4°C with $R_{\odot}=0$, estimates the critical T_b at which *V. atalanta* males depart. Even on sunny days there was much variance in end time ($R^2=0.26$, $F=13.93$, $P<0.0006$, $n=41$). The best-fitting exponential curve for sunny days (Fig. 4) parallels the T_b isotherms when T_a is low, but levels off at higher T_a .

When wind velocity (V_w) is higher, *V. atalanta* males decamp when solar radiation levels are higher (Table VIII). This relationship holds on clear (multiple regression by cloud cover, Table IX) and cumuliform-clouded days. There was no correlation of FREQ with variation in the T_a - R_{\odot} relationship (Table VIII), nor was FREQ correlated with V_w ($r=-0.14$, $P=0.17$).

Interaction Frequency and Waiting Time

V. atalanta males wait longer in their territories after end dance when \log_{10} FREQ is lower (linear regression; $R^2=0.09$, $F=20.34$, $P<0.0001$, $n=196$). Waiting time varied by the formula 0h.58 - 0.19 \log_{10} FREQ (Fig. 5). This relationship, however, was significant only because it was so on overcast days ($R^2=0.17$, $F=8.89$, $P=0.0047$, $n=45$), when waiting time varied by the formula 0h.75 - 0.30 \log_{10} FREQ. On clear days the relationship was only approaching significance ($R^2=0.04$, $F=3.63$, $P=0.0598$, $n=97$), and was insignificant under cirroform or cumuliform clouds.

Table VIII. End Time Solar Radiation^a vs. Ambient Temperature, Cloud Cover, Wind Velocity, and Interaction Frequency.

Source	df	SS	<i>F</i>	<i>P</i>
Ambient temp. (T_a)	1	17647.06	43.89	<0.0001
Wind velocity (V_w)	1	8458.30	21.04	<0.0001
Cloud cover	3	1655.22	1.37	0.2566
Interaction frequency (FREQ)	1	2.95	0.01	0.9319

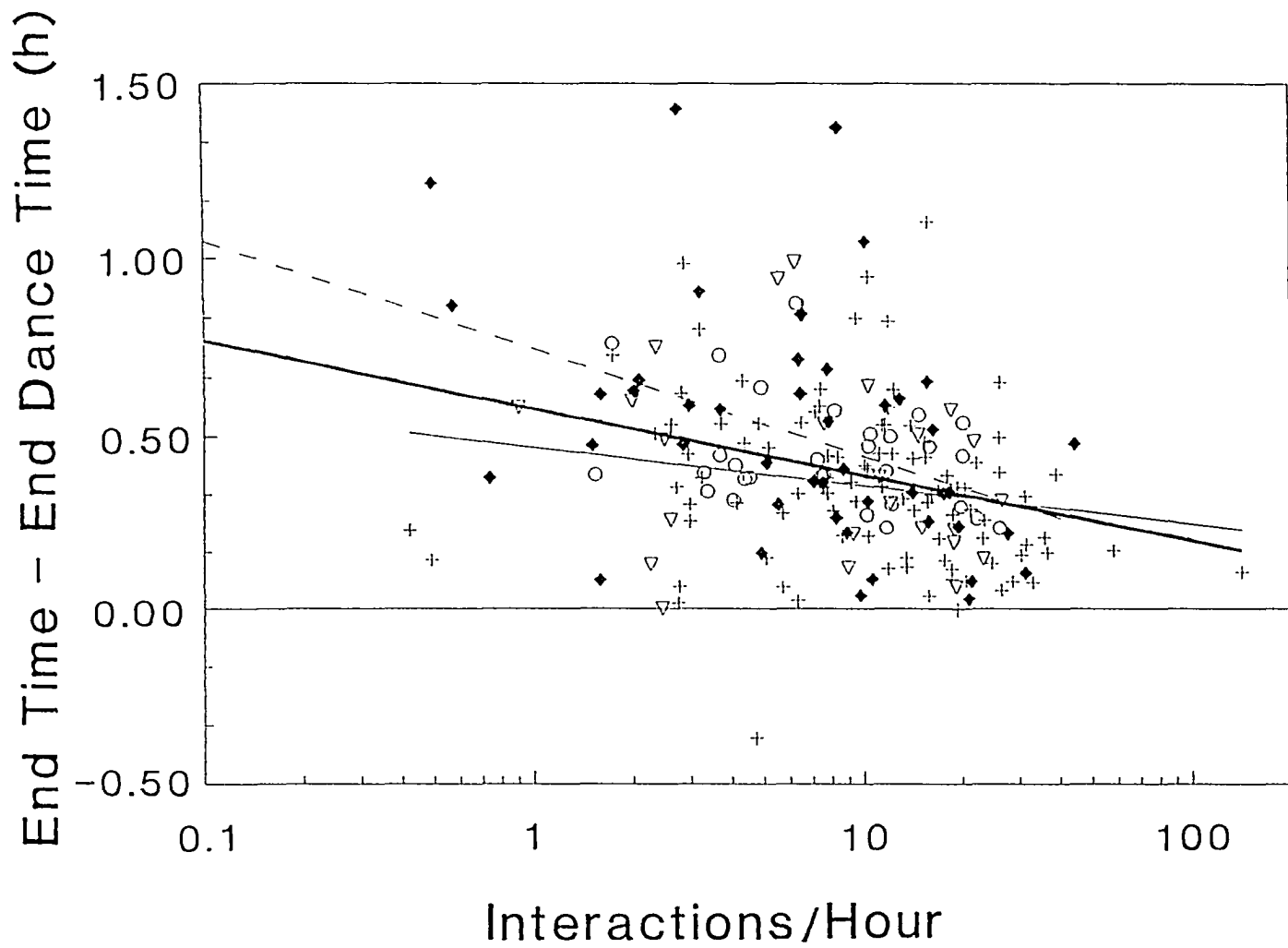
^aEnd time $R_{\odot} = 121.08 - 4.97 T_a + 14.92 V_w$. $R^2 = 0.41$, $F = 9.94$, $P < 0.0001$, $n = 94$, 6 treatment df.

Table IX. End Dance Solar Radiation^a vs. Ambient Temperature, Wind Velocity, and Interaction Frequency on Overcast Days.

Source	df	SS	<i>F</i>	<i>P</i>
Ambient temp. (T_a)	1	2946.98	9.80	0.0053
Wind velocity (V_w)	1	1266.71	4.21	0.0535
Interaction frequency (FREQ)	1	97.22	0.32	0.5761

^aEnd time $R_{\odot} = 107.60 - 4.64 T_a + 11.22 V_w$. $R^2 = 0.40$, $F = 4.43$, $P < 0.0152$, $n = 24$, 3 treatment df.

Figure 5. Relationship of interaction frequency (FREQ) to waiting time after end dance. Sky conditions and the corresponding regression lines are indicated as in Fig. 2. All conditions: Waiting time = $0\text{h}.58 - 0.19 \log_{10} \text{FREQ}$, $n=196$. Clear sky: Waiting time = $0\text{h}.46 - 0.11 \log_{10} \text{FREQ}$, $n=97$. Overcast: Waiting time = $0\text{h}.75 - 0.30 \log_{10} \text{FREQ}$, $n=45$.



Mean duration of waiting time on all days was $0\text{h}.41 \pm 0\text{h}.26$; for non-overcast days, $0\text{h}.38 \pm 0\text{h}.23$. An ANCOVA model using FREQ ($R^2=0.16$, $F=2.49$, $P=0.0029$, $n=198$) showed that waiting time was not correlated with T_a ($F=0.01$, $P=0.93$), with year ($F=1.83$, $P=0.11$), or with departure mode ($F=1.16$, $P=0.33$). Correlation of cloud cover with waiting time was approaching significance ($F=2.42$, $P=0.0672$), with waiting time possibly being longer on overcast days (adjusted mean= $0\text{h}.33$) than on clear days ($0\text{h}.21$).

DISCUSSION

Excluding seasonal effects, departure or end time of *V. atalanta* territorial occupants is correlated primarily with end dance time, secondarily with ambient temperature and third most strongly with interaction frequency. As T_a increases, end time gets later, presumably because less heat is needed from R_{\odot} . The sun's altitude is lower later in the day and less radiational heat is available. As with start time (Bitzer and Shaw, 1995), and end dance time (Bitzer and Shaw, in preparation), end times are earlier in spring and late summer than in mid-summer because the sun then reaches a particular altitude earlier in the afternoon. Because EDSA was confounded with the other three independent variables, we could not determine the extent to which these affected end time directly, as opposed to indirectly by affecting end dance time. The relative importance of end dance time vs. climatic factors was also ambiguous. Whereas the first principal components analysis seems to establish the primacy of EDSA over T_a and FREQ, the second, incorporating more factors, points to T_a as the most important factor correlated with end time. Resolving this question requires an experiment such as releasing captive males over an occupied

territory after the presumptive end dance time to find out whether end time is then delayed as a result. Sorting out the relative importance of some climatic factors such as R_{\odot} and T_a to end time might be done by exposing perched *V. atalanta* occupants to artificial light or heated substrates. In one suggestive observation, an occupant perched beneath a walkway light where the luminance measured 7 foot-candles continued dorsal basking and failed to decamp for at least 1 h after the expected end time.

End time varies by nearly the same amount per °C of T_a as does end dance time, as the respective T_a coefficients indicate. End time = $14\text{h}.40 + 0.094T_a + 0.089\delta + 2.54\epsilon + 0.005(\text{FREQ})$, whereas end dance time = $14\text{h}.25 + 0.087T_a + 0.078\delta + 2.58\epsilon + 0.012(\text{FREQ})$, (Bitzer and Shaw, in preparation). The variance of end time (Table I) ($R^2=0.65$) is also similar to that of the comparable end dance time model ($R^2=0.66$, $F=52.17$, $P<0.0001$, $n=198$, Bitzer and Shaw, in preparation). Slopes of the linear regression lines for end time ($= 15\text{h}.92 + 0.13T_a$) and for end dance ($= 15\text{h}.56 + 0.13T_a$) were similar, as were the corresponding lines for each sky condition. The nearly parallel lines indicate that the interval between end time and end dance is almost constant over a wide range of T_a under different types of cloud cover, a point we will discuss further.

Interrelationship of Ambient Temperature, Solar Radiation, Wind Velocity, and Interaction Frequency Effects

V. atalanta males, like non-territorial *A. paphia* (Vielmetter, 1958), may utilize R_{\odot} and T_a to determine when to decamp from their territories and fly to roost. Nevertheless, the regression line showing mean T_a and R_{\odot} at end time on sunny days spans a broad range of the T_b values measured for dorsally-

basking dead *V. atalanta* males. This contrasts with *V. atalanta* start time which occurs when T_b drops to a narrow range of levels (Fig. 5; also see Bitzer and Shaw, 1995). Since the declining light (diffuse R_\odot) levels near dusk inhibit butterfly activity, even if T_a is favorable (Douwes, 1976; Saunders, 1982; Rawlins and Lederhouse, 1978; Dennis, 1993, p. 31), *V. atalanta* males' departure may be an isothermal response at low T_a , but be increasingly limited by oncoming darkness when end time occurs around or after sunset at higher T_a . The exponential curve depicted in Fig. 5 would then more accurately represent the true T_a - R_\odot relationship for end time. Alternately, since end dance time may depend similarly on low light level (Bitzer and Shaw, in preparation), and waiting time tends to be constant, the end time curve may simply parallel that for end dance. Correlations of other secondary variables such as FREQ with end time may likewise be an after-effect of a real effect of FREQ upon end dance.

At any rate, one cannot necessarily assume that seemingly linear T_a - R_\odot equations indicate an isotherm for equilibrium T_b , especially if they occur near dawn or dusk when solar radiation decreases non-linearly with solar altitude.

Bitzer and Shaw (in preparation) suggest that the much less rapid decrease per °C of T_a in the critical R_\odot at end dance time as compared with that at start time may be partly due to flying butterflies being less responsive to R_\odot than dorsally basking butterflies. This may also be so near end time, when perched butterflies invariably rest with wings closed. The equilibrium T_b of dead butterflies with closed wings varies similarly with R_\odot ($T_b = 0.0096R_\odot + 1.38T_a - 6.55^\circ$) as does that of dead butterflies suspended in gliding position [$T_b = 0.0099R_\odot + 1.10T_{a160\text{ cm}} - 2.10^\circ$] Bitzer and Shaw, in preparation]. In

comparison, the equilibrium T_b of dorsal baskers = $0.034R_{\odot} + 1.19T_a - 3.42^{\circ}$ (unpublished data). These R_{\odot} coefficients indicate that both closed and suspended butterflies warm up by only one-third as much in sunshine as do dorsally basking ones.

R_{\odot} levels are much lower at end time than at start time. The critical $R_{\odot} = 141.73 \text{ W/m}^2 - 5.20T_a$ at end time on sunny days, whereas at start time, $R_{\odot} = 1557.46 \text{ W/m}^2 - 41.94T_a$. Since *V. atalanta* males maintain a similar T_a - R_{\odot} relationship for end time on overcast as well as sunny days (Fig. 4), end time, like end dance (Bitzer and Shaw, in preparation) and unlike start time (Bitzer and Shaw, 1995), may be largely a response to radiation level as Vielmetter (1958) found for *A. paphia*. Alternatively, *V. atalanta* males may simply wait for a relatively constant interval after the end dance. Whatever the cause, perched *V. atalanta* males decamp earlier on overcast days when similar R_{\odot} levels occur correspondingly earlier. The difference between clear and overcast days is greater when T_a is lower (Fig. 2).

Since occupants' tendency to leave territories under overcast seems to depend on climatic factors in the same way as on sunny days, a circadian rhythm modulated by T_a and possibly other climatic factors (see Bitzer and Shaw, 1995) is not needed to explain the end time schedule, but cannot be ruled out by these data. The much greater difference between end times under overcast vs. clear sky (Fig. 2) on cooler days indicates that *V. atalanta* males then depend upon R_{\odot} much more than they do on warmer days.

Effects of Wind Around End Time

Although critical R_{\odot} levels for departure seem to be higher on windier days, there is no corresponding correlation of V_w with end time itself. Lack of an unambiguously significant effect of V_w upon both end time and start time (Bitzer and Shaw, 1995) contrasts with the correlation between V_w and end dance time (Bitzer and Shaw, in preparation). In Bitzer and Shaw (1995), we attributed lack of a V_w effect upon start time partly to V_w being much lower near the ground (Campbell, 1977, pp. 37-40). *V. atalanta* occupants often patrol within their territories after end dance, suggesting they continue to benefit from these more sheltered conditions near the ground (see Alcock, 1985). *V. atalanta* occupants preparing to decamp from their perches on the ground should likewise be less affected by wind. Factors such as thermal stabilization of the boundary layer as sunset approaches, and the resulting lack of near-ground turbulence (Takle *et al.*, 1976) do not seem to increase correlation of end time with V_w . Polcyn and Chappell (1986) stated that wild *V. cardui* perched on the ground when R_{\odot} is high probably experience substantial turbulence, which may not vary in proportion with V_w . This might make start time unpredictable from V_w . But near end time, with little turbulence in a laminar air layer, even butterflies on the ground could respond proportionally to V_w as measured higher up. Nevertheless, they do not seem to do so.

How Soon Should Occupants Leave Their Territories?

One would expect that *V. atalanta* males would benefit most by leaving their territories as soon after end dance as possible. If end dance time were highly predictable by T_a and other climatic factors alone, this would be the most

efficient strategy. Once the last intruder had passed through a territory, the occupant would still be warm enough to fly vigorously to a roost site because it had been perched (see Alcock, 1985). It might note its own dropping T_b while resting or patrolling, then quickly fly off to roost. Arrival time of the last male *V. atalanta* intruder at a territory followed by a sufficiently long interval when no intruders arrive probably indicates accurately to the occupant the latest time at which a female is likely to fly by. 196 of 198 (99.0% of) end times occurred after the last vagrant had flown through the territory. Heating of both sexes of *V. atalanta* is probably similar. Pivnick and McNeil (1986) suggest that sexual dimorphism in size and thermoregulation are not advantageous to perching species, since females must also fly for mating to occur. This situation contrasts with that of some patrolling butterflies such as *Thymelicus lineola*, in which the larger yet relatively shorter-winged females (Dennis, 1993, Pivnick and McNeil, 1986,) must maintain a somewhat higher T_b and faster wingbeat than do the males in order to fly with similar efficiency.

Thus, if end dance time depended strongly upon climatic factors, occupants should likewise use mainly climatic cues to decide when to fly to roost, and the time between end dance and end time should then be minimal.

V. atalanta males may wait in their territories for a longer period after the last intruder has passed because end dance time strongly depends upon population density as well as climate (Bitzer and Shaw, 1995). With a "spillover" of late-arriving males on days when many vagrants are active, end dance may come later than a *V. atalanta* occupant would be able to predict from his own T_b and internal state. Since end dance time is rather unpredictable and occupants cannot be certain that any one intruder will indeed be the last, they

may benefit by waiting longer in their territories. On overcast days and possibly on clear days they may use interaction frequency as a cue to discern yet how much longer to remain there to await females. Perhaps surprisingly, occupants then wait longer after end dance if the mean interval between intruders is longer. This strategy would seem to be counterproductive, unless these occupants are unlikely to occupy territories on subsequent days, and/or females are in such short supply that it pays for males to wait longer for more infrequent arrivals rather than leave. On other days they seem to wait for a relatively fixed period of time before leaving, regardless of T_a or $FREQ$. Our alternative hypothesis that *V. atalanta* males should wait longer after end dance to leave when $FREQ$ is high and many males (and presumably females) are active, is thus rejected.

Since *V. atalanta* males have often invested much time and effort holding their territories already as end time approaches, they may continue to stay there for that reason as well. This is the "dollar auction" strategy (Poundstone, 1992). Thus low rates of occupant turnover and longer periods of occupancy by individual males may correlate with their waiting for longer periods of time after what is presumably the last interaction. Territorial *Polygonia comma* males typically stay in a particular territory for only 10-20 min before moving on (unpublished data), and 12 or more individuals may occupy one site in a 2.5-3 h period. *P. comma* males also tend to wait only ca. 10 min (0h.17) after end dance before leaving, and occupants sometimes leave a territory before the last vagrants have passed through it (unpublished data). *V. atalanta* males seem generally more persistent; from one to seven males may hold a territory during the territorial period.

There should also be a trade-off between the decreasing benefits of staying longer to wait for a late-arriving female, and the ever-growing risks of cooling off too much to leave the perch, avoid ground-foraging birds, chameleons [in Florida (Swanson, 1979)], or patrolling bats, or efficiently seek a roost site. *V. atalanta* males might tend in different locations to leave earlier or later depending upon whether or not crepuscular predators are actively seeking them.

Interspecific Interactions and End Time

Interspecific interactions between sympatric species (Bitzer and Shaw, 1983, Gaugler and Schutz, 1989) may have relatively little effect upon when such late-leaving species decamp from their territories. Since *V. atalanta* males depart and roost from very late afternoon to twilight, there are no other butterfly species which start activity when *V. atalanta* activity is winding down. This contrasts with the situation for *P. comma*, which typically decamps 1.5-2.5 h earlier when the numbers of vagrant *V. atalanta* males are still rising (Bitzer and Shaw, 1983; unpublished data). We have thus seen territorial *P. comma* males waste considerable energy chasing large numbers of vagrant and perching *V. atalanta* flying through their territories later in the day.

The time when each occupant decamps from its territory to seek a roost is more predictable from the end dance time than it is from T_a and other climatic variables. We also believe that correlations of climatic variables with end time may be mainly an artifact of their correlation with end dance, which itself affects end time more directly. *V. atalanta* males seem to leave their territories in response to a chain of earlier events which also depend upon both climatic factors and population density. Although start time depends greatly upon

climate and seemingly little upon population density, the effects of vagrant male population densities apparently compound over the territorial period and may predominate over climatic factors at the end. End time is thus potentially more complex than the simple "change of state" that Vielmetter (1958) described for *A. paphia* flying into overhead branches to roost for the night.

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SECTION II. TERRITORIAL CONTESTS

CHAPTER 4. TERRITORIAL INTERACTIONS OF THE RED ADMIRAL,
Vanessa atalanta (LEPIDOPTERA: NYMPHALIDAE):
LARGER BUTTERFLIES, OCCUPANTS, AND CHASERS USUALLY WIN

A paper to be submitted to *Animal Behaviour*

Royce J. Bitzer^{1,2} and Kenneth C. Shaw¹

ABSTRACT

Vanessa atalanta males are territorial in late afternoons from late April to late August or early September. The typical male-male interaction is an ascending helical chase lasting from several seconds up to more than a minute. We examined the effects of both strategic and climatic factors upon both the duration and outcome of interactions. We found that the larger the occupant relative to the intruder, the more likely it was to win. Small occupants fighting large intruders, however, did better than small intruders against large occupants, indicating prior occupancy is also important. Butterflies which chased were also more likely to win than those which were chased, and occupants were more likely to yield to intruders on warmer days. Interaction duration was longer when occupant and intruder were more nearly equal in size, when the intruder chased the occupant, and on cooler days. Duration of interactions, however, did not affect their outcome. The effect of ambient temperature upon both outcome and duration was relatively small compared to

¹Graduate student and Associate Professor, respectively,
Department of Zoology and Genetics, Iowa State University.

²Author for correspondence.

those of butterfly size, prior occupancy, and chase position.

INTRODUCTION

A number of studies (Baker, 1972; Davies, 1978; Bitzer & Shaw, 1979; 1983; Wickman, 1985; Rosenberg and Enquist, 1991) present evidence that counters Scott's (1974) claim that butterfly males do not occupy and defend sites and therefore are not true territorial species. Baker (1972) and Rosenberg and Enquist (1991) suggest that serious consideration of territorial behavior in butterflies has been hindered by lack of evidence that butterflies are equipped to inflict injury on one another, i.e., how could territorial behavior evolve if contestants can't injure one another? Wing damage during aerial encounters is, however, a likely risk for butterfly males. We have seen and heard red admiral (*Vanessa atalanta*) males wing beating during aerial encounters (unpublished observations). Rosenberg & Enquist (1991) report a few similar observations for another nymphalid, *Limenitis weidemeyerii*, and Thornhill and Alcock (1983) refer to a report by Eff (1962) of severe wing damage by males of the swallowtail, *Papilio indra*, during aerial fights. Pinheiro (1991) observed that territorial males of the swallowtails *Eurytides orthosilaus* and *Papilio thoas* sometimes grapple in mid-air and fall to the ground. The butterflies hold each other by the legs and often by the claspers as well. Depending upon the height and place of the fall, serious wing damage can result (Pinheiro, 1991).

If butterflies are truly territorial, their territorial behavior should follow contest rules and strategies adopted by occupants and intruders (Enquist & Leimar, 1983). These include the following: 1) larger and/or stronger animals should occupy most territories, 2) the greater the differences in size and strength

of combatants, the shorter the contest, and 3) given animals of equal size, occupants should win more contests than intruders (Maynard-Smith & Parker, 1976; Leimar & Enquist, 1984).

Occupancy advantage may occur for several reasons. The most likely reason is the time and effort that the occupant has invested in the territory. Visual knowledge of the details of a territory might also give an occupant an advantage. For example, *V. atalanta* males drive intruders upward in an aerial spiral which ends among the top branches of trees associated with the territorial site. *Inachis io* and *Aglaia urticae* occupants chase intruders far away from territories, so that intruders have a more difficult time relocating the territory than do occupants who have returned previously (Baker, 1972). Besides expecting occupants to win more often over intruders of equal RHP, one would also predict that relatively small occupants would win more contests over large intruders than vice-versa.

When does a butterfly decide to leave a contested site? Vagrant males could estimate the size of territorial occupants from a distance and simply decide not to intrude. However, once a vagrant male becomes an intruder, a close encounter resolves the contest. Such encounters are typically aerial chases of various forms. A butterfly most likely decides to leave during such interactions.

Microclimatic factors which affect duration of territorial interactions might also affect their outcome. Wickman & Wiklund (1983) found that *Pararge aegeria* interactions were shorter at higher ambient temperatures (T_a). Wickman (1985) found that *Coenonympha pamphilus* interactions lasted longest in the morning and the afternoon when the air was cooler and males showed the greatest tendency to perch. They were shortest at midday when males were

most likely to patrol in search of mates. Wickman & Wiklund (1983) suggested that sunspot-based territories become less valuable to *P. aegeria* at warmer temperatures because females then have less need to bask in sunspots. Interactions should thus become shorter either because occupants strive less to keep their territories, or because intruders strive less to capture them, or both.

Other factors such as solar radiation and substrate temperature (T_s) (Shreeve, 1984; Wickman, 1988) may also affect interaction duration by imposing thermal constraints upon flight or by affecting the attractiveness of perching as a strategy.

One question which needs to be examined more closely is whether or how much duration of a territorial interaction affects the chance that an occupant will win. With the nymphalids *Inachis io* and *Aglaia urticae* (Baker, 1972), occupants were more likely to drive off intruders if they spent more time chasing intruders further from the territory (at increasing risk of not returning before the next intruder arrived.)

This study parallels that of Rosenberg & Enquist (1991) in determining how size and occupancy affects territorial contests of the nymphalid butterfly, *V. atalanta*. We also explore the relationship between chase position and microclimatic factors on contest outcome.

MATERIALS AND METHODS

Territorial *V. atalanta* males were observed at four sites on the Iowa State University campus between late April or early May to mid-August or early September from 1987 to 1989. The beginning and end of each spiral interaction (Bitzer and Shaw, 1979) and the time when the winner landed back in the

territory were recorded to the nearest second with a quartz watch kept set to WWV time signals. Microclimatic conditions were recorded as in Bitzer and Shaw (1995), and the thermometer was read every 5-20 min throughout the entire 2-3.5 hours of the late afternoon territorial period.

Territorial interactions were observed from the side or from directly below. There are three types: 1) brief hovering interactions of ca. 1-7 s, after which occupant and intruder separate, 2) horizontal chases of 5-10 m, 0.7-1.8 m above the ground, and 3) spiral interactions lasting from 5-70 s, in which the two butterflies circle up to treetop height (10-15 m) before one butterfly drives the other off over the treetops.

Only spiral interactions were observed because they are more likely to be "true contests" in the sense of Wickman and Wiklund (1983), and because their generally longer duration allowed us to distinguish and observe the interacting butterflies during a spiral flight, much as did Baker (1972). With practice, we could soon distinguish occupant from intruder, relative sizes of the two butterflies, and whether the occupant chased or led in the interaction. We recognized five classes of relative occupant size: 1) smaller; 2) slightly smaller; 3) equal to; 4) slightly larger, and 5) larger than the intruder. When butterflies reversed chase positions during a spiral flight, we used the final position in our analyses. We also noted the times when the interaction began, when the contestants separated, which butterfly won, and when the winner landed on his perch. Ties occurred when both butterflies returned and started another interaction in mid-air, neither of them having relit on the perch; when both butterflies relit in the territory after an interaction; or when neither butterfly returned to the territory. A butterfly was said to win an interaction whenever

he was the only one of the pair to light in the territory, however briefly. A payoff index, indicating proportions of wins (3 pts.), ties (2 pts.), and losses (1 pt.) for different size classes, was calculated from the formula

$$\text{Payoff index} = \frac{1(\# \text{ losses}) + 2(\# \text{ ties}) + 3(\# \text{ wins})}{\text{total \# of interactions.}}$$

Interactions involving three or more butterflies were excluded from the sample, as were observations in which occupant and intruder were not clearly distinguishable. Because relative size was one factor which allowed us to distinguish butterflies in flight, we note a potential source of bias. Proportionately more observations in which the two butterflies were of equal size may have been discarded.

Besides the three strategic factors of size, occupancy, and chase position, we also examined the effects of microclimate, specifically ambient temperature (T_a), upon interaction duration and outcome. We also included the waiting time, the number of seconds a butterfly had been resting on his perch before each interaction, to see whether or not occupants flew longer interactions after having perched or basked for longer periods of time.

We analyzed data with both χ^2 and multiple regression analyses. The multiple regressions yielded numerical mean payoff values (based upon proportions of wins, ties, and losses) for different relative sizes of occupants and intruders, and compared the importance of strategic and climatic variables. Interactions for which we obtained only one or two of the three strategic observations were included in the appropriate χ^2 analyses. Total numbers of interactions used in different χ^2 analyses were therefore different. Only

complete observations including relative size, outcome, position, waiting time, and T_a were included in the multiple regression models.

Since *V. atalanta* is a migratory species, we were rarely able to re-observe marked occupants and intruders of known size as did Rosenberg and Enquist (1991). We therefore compared the wing lengths and masses of occupants and intruders as groups during 1990. If larger butterflies tend to occupy territories more frequently than smaller ones, then occupants should on average be larger and heavier than butterflies in a sample of the general population.

To sample the general population, we first removed the current occupants from an active site to exclude them from the sample. We then netted incoming butterflies before they could pitch in the territory or interact with other incoming males. (Any that did so before capture were excluded from the sample, unless they were caught in mid-air during their first interaction. Then both butterflies were kept.) Each butterfly was placed in a separate labeled container. After butterflies stopped arriving, they were weighed, measured, and marked in the laboratory.

Butterflies were anesthetized by chilling them to 2°C in a walk-in refrigerator. The longest axis of the forewing was measured with calipers and a ruler to the nearest 0.1 mm as in Lederhouse (1982). They were then weighed in a flat-black plastic cup on an electronic balance to the nearest 0.001-0.0001 g, and the cup weight was subtracted. After being numbered with orange Testor's® model airplane enamel on the underside of the left hindwing, they were released into a flight cage and allowed to warm up fully. The butterflies were then released into roost trees near the territorial site later the same night. We thus obtained the weight and size distribution of the general population.

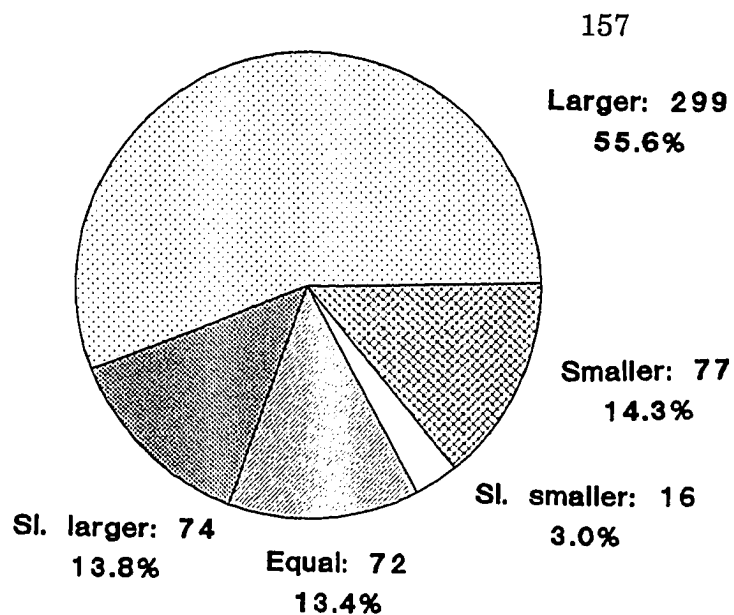
To gather a sample of successful territorial occupants, we visited a number of territories in succession. One occupant was removed from each territory, but only after it had been observed to win one bout with an intruder (usually 1-5 interactions). We also waited until males became well-established in their territories. We observed several start times, then waited ca. 30 min before sampling. Each butterfly was again placed in an individual container, measured and weighed as before, and was then numbered as before with yellow enamel. Each of the butterflies was then released into a roost tree near the territory from which it was taken. This sample showed the size and weight distribution of males which have successfully held a territory.

RESULTS

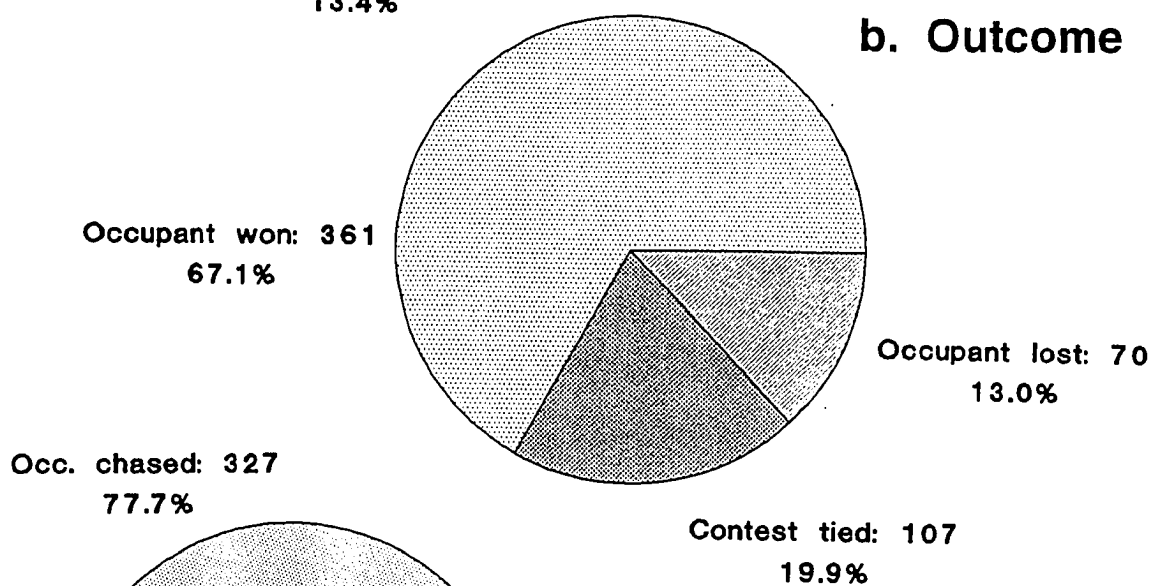
Characteristics of Territorial Occupants

Occupants were larger in 69.3% of interactions (373 /538) ($\chi^2=214.17$, $P<0.0001$, 3 df); in 80.2% (299/373) of these cases, occupants were considerably larger (not "slightly larger") than intruders (Fig. 1a). Occupants won 67.1% of interactions (361/538; $\chi^2=279.87$, $P<0.0001$, 2 df) (Fig. 1b) and chased intruders during 77.7% of interactions (327/421; $\chi^2=279.87$, $P<0.0001$, 2 df) (Fig. 1c). The above values are averaged over three years of observations; there was no significant difference among years.

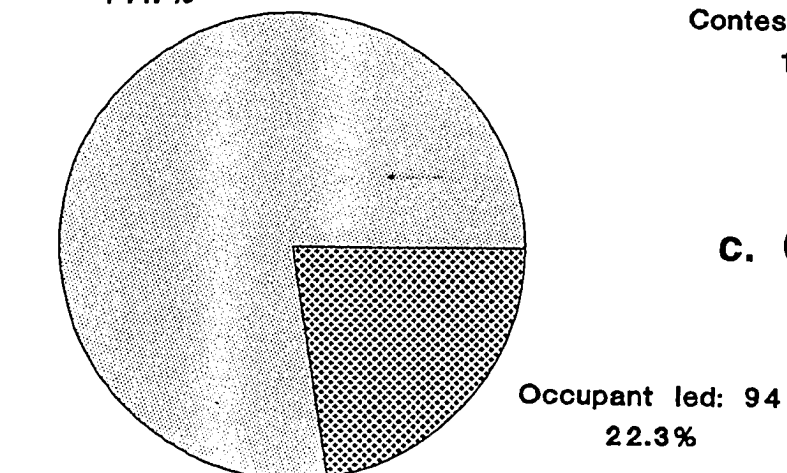
Figure 1. a. Numbers and percentages of *V. atalanta* spiral interactions in which the occupant was larger than, slightly larger than, equal in size to, slightly smaller than, and smaller than, the intruder. Total number of interactions = 538. **b.** Numbers and percentages of *V. atalanta* territory occupants which won, tied in, or lost spiral interactions. Total number of interactions = 538. **c.** Numbers and percentages of *V. atalanta* occupants which chased or led in spiral interactions. Total number of interactions = 421.



a. Relative Size



b. Outcome



c. Chase Position

Correlations of Butterfly Size and Occupancy with Outcome and Chase Position

The Relative Importance of Size and Occupancy in Determining Interaction Outcome

Size was more important than occupancy in determining interaction outcome; both larger occupants and larger intruders won more frequently than smaller opponents (Fig. 2). However, occupancy was also important; larger occupants won a considerably greater percentage (81.8%) of interactions than larger intruders (46.2%). In addition, when occupant and intruder were equal in size, occupants won 54.2% while intruders won only 14.9% of interactions. Similarly, small occupants won 30.1% while small intruders won only 5.3%. There was no significant difference in relative size vs. outcome between the three years ($\chi^2=5.89$, $P > 0.20$, 4 df). Model $\chi^2=143.25$ ($P<0.0001$, $n=538$, 6 df)

Payoff indices for the five relative size classes of occupants (Table I, Fig. 3) likewise show that larger occupants tend to win higher proportions of interactions. The corresponding index for large intruders challenging small occupants is only 2.17, meaning that they do only slightly better than do occupants fighting equal-sized intruders.

The Relative Importance of Size and Occupancy in Determining which Butterfly Chases during Spiral Interactions

In contrast to interaction outcome, occupancy was more important than size in determining which butterfly chased (Fig. 4). Regardless of size difference, occupants chased intruders more frequently than vice versa. Smaller as well as larger occupants chased more than they were chased although the difference between smaller occupants and larger intruders was not significant ($\chi^2 = 2.05$, $P=0.16$, $n=59$, 1 df) (Fig. 4). Size, was also important, however;

Figure 2. Interaction outcome vs. relative size of occupant. Numbers of interactions are shown above the bars, which indicate absolute numbers of wins, ties, and losses. Data from the categories "occupant slightly smaller" and "occupant smaller " have been lumped under the heading "smaller." Relative size classes and outcomes of intruders can also be inferred from the graph: e.g., the number of times which smaller occupants lost (43) was also the number of times which the larger intruders they had fought had won. $\chi^2 = 143.25$, $P < 0.0001$, $n = 538$, 6 df.

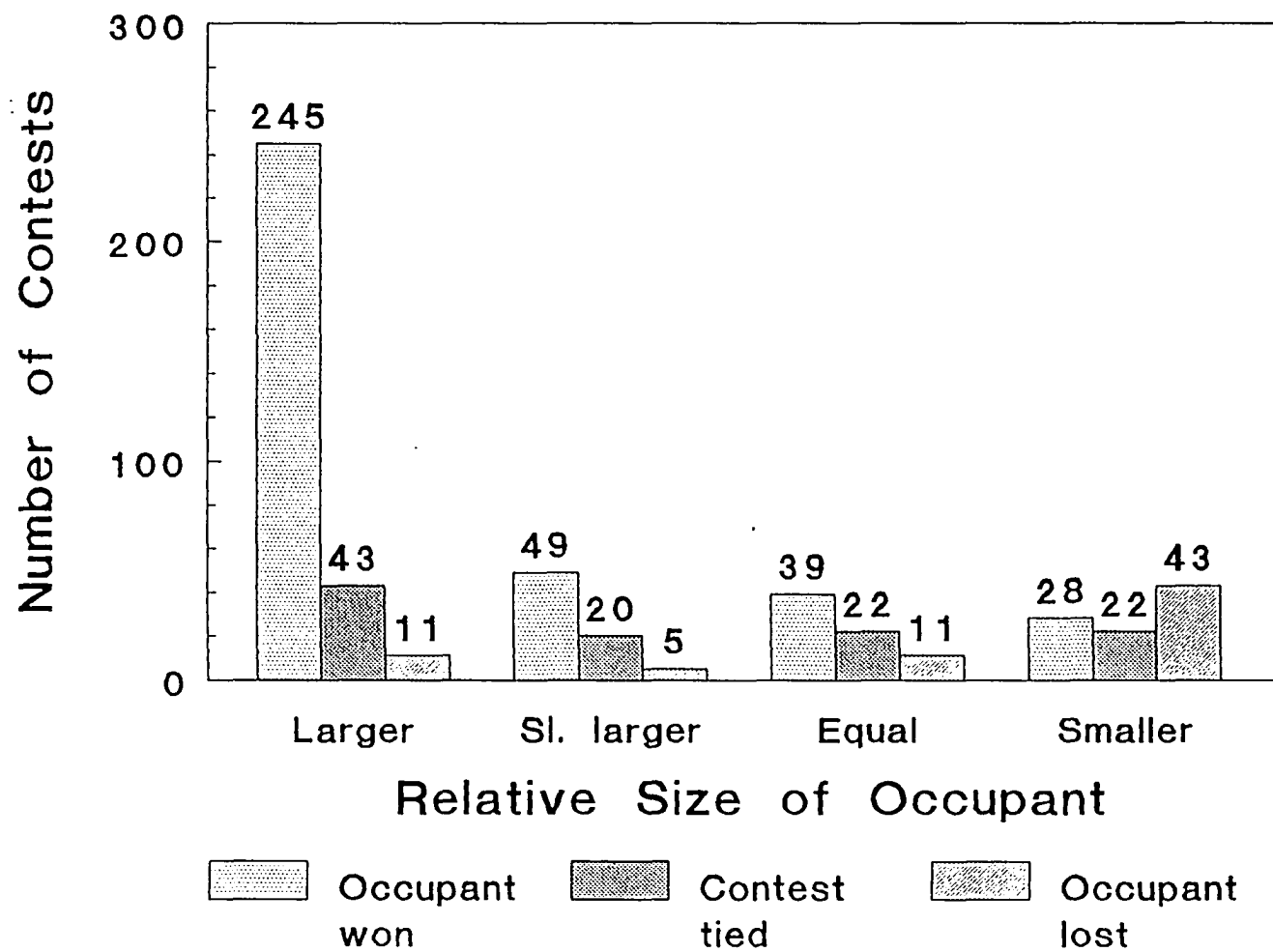


Table I. Correlation of Interaction Outcome (Payoff Index^a) with Relative Size, Chase Position and Duration, Ambient Temperature, Resting Time, and Julian Date.

Source	df	SS	<i>F</i>	<i>P</i>
Relative size	4	39.12	28.40	<0.0001
Chase position	1	8.08	23.47	<0.0001
Chase duration	1	0.10	0.29	0.5915
Ambient temp. (T_a)	1	1.69	4.89	0.0275
Resting time	1	0.50	1.45	0.2293
Julian Date	1	0.83	2.40	0.1225

Relative size of occupant	Adjusted mean payoff index	Payoff difference	Different from larger? <i>t</i>	<i>P</i>
Smaller	1.82	-0.87	-9.65	<0.0001
Slightly smaller	1.88	-0.81	-4.65	<0.0001
Equals intruder	2.10	-0.59	-3.46	0.0006
Slightly larger	2.47	-0.23	-2.74	0.0063
Larger	2.70	0	-	-

Chase position of occupant	Adjusted mean payoff index	Payoff difference	Different from chasing? <i>t</i>	<i>P</i>
Being chased	2.02	-0.36	-4.84	<0.0001
Chasing	2.37	0	-	-

^aPayoff index = 3.07 + Relative size payoff difference + Chase position payoff difference - 0.022 T_a . $R^2 = 0.31$, $F = 19.61$, $P < 0.0001$, $n = 397$, 9 treatment df.

Figure 3. Mean interaction outcome (payoff index) vs. relative size of occupant. Payoff indices, shown above the bars, were calculated by scoring a loss as 1 point, a tie as 2 points, and a win as 3 points, using the formula

$$\text{Payoff index} = \frac{1(\# \text{ losses}) + 2(\# \text{ ties}) + 3(\# \text{ wins})}{\text{total \# of interactions.}}$$

Payoff indices for the corresponding intruders = 4 - the occupant payoff index, e.g., the payoff index for larger intruders fighting smaller occupants = 4 - 1.82 = 2.18. $n = 538$.

Mean Interaction Payoff Index

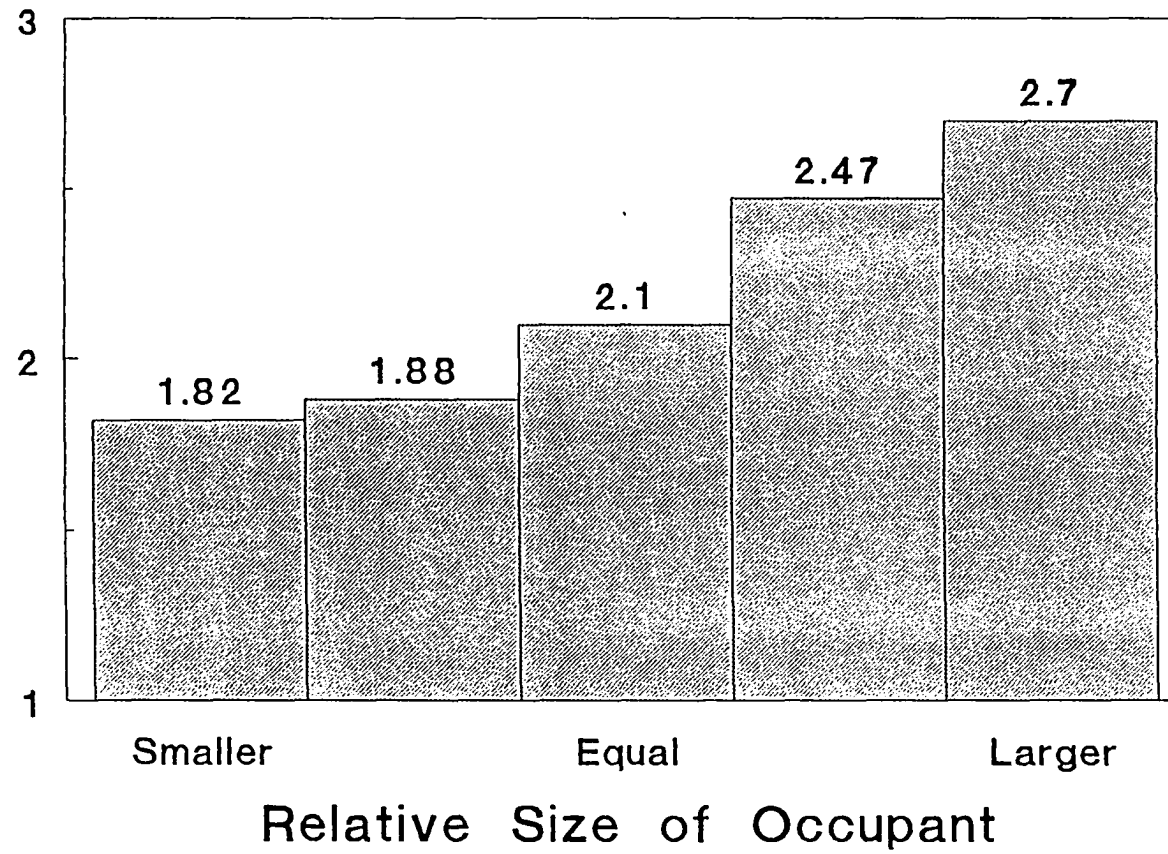
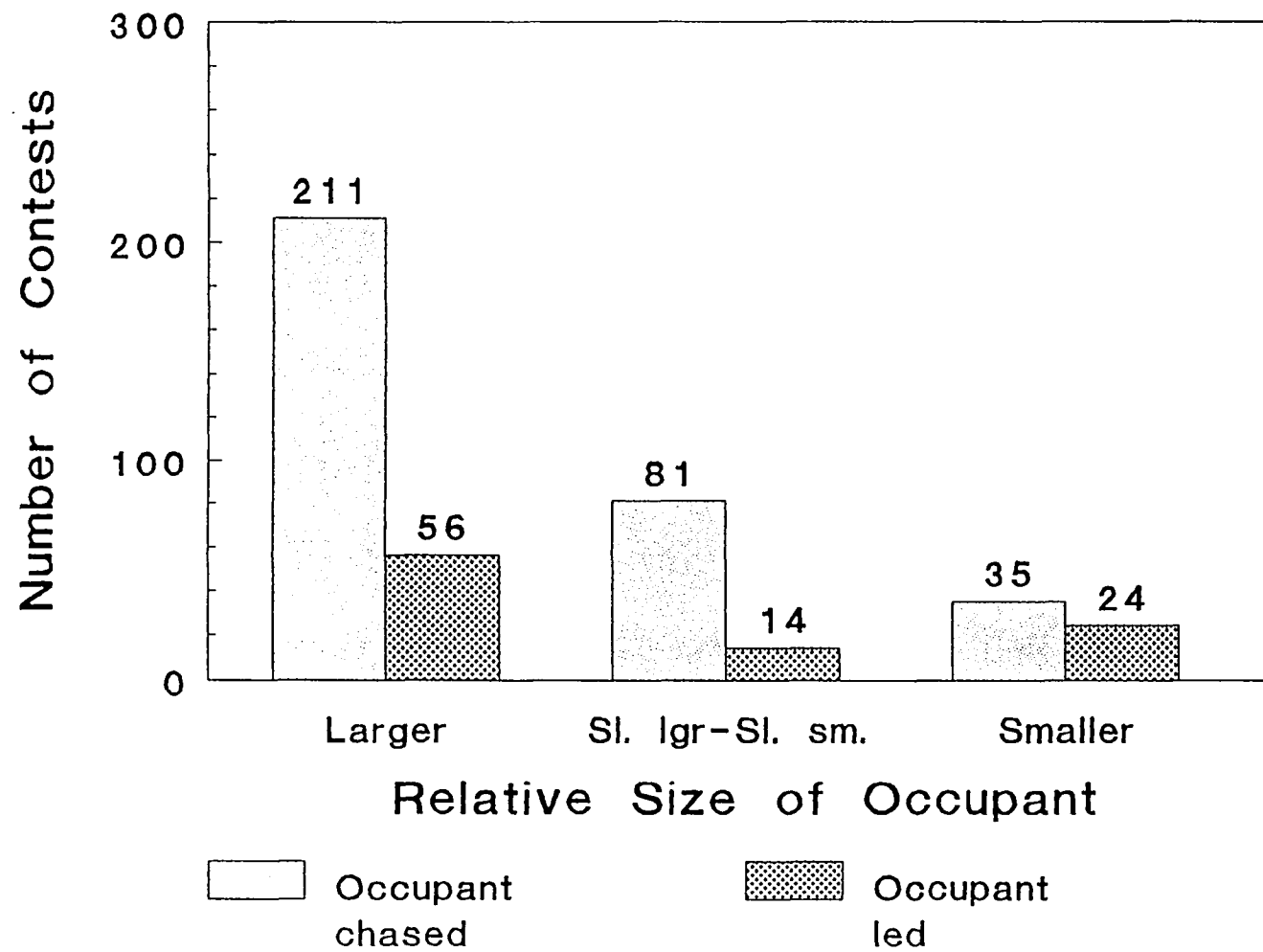


Figure 4. Chase position in interactions vs. relative size of occupant. Numbers of interactions are shown above the bars, which indicate absolute numbers of chasing and leading interactions. Data from the categories "occupant slightly larger," "equal" and "slightly smaller " have been lumped under the heading "slightly larger - slightly smaller," due to low numbers of interactions in which the contestants differed slightly in size. Relative chase positions and outcomes of intruders can also be inferred from the graph: e.g., the number of times which smaller intruders led (24) was also the number of times which the larger intruders they had fought had chased them. $\chi^2 = 14.89$, $P < 0.001$, $n = 421$, 2 df.



smaller occupants chased larger intruders considerably less frequently (59.3% [35/59]) than large occupants chased smaller intruders (80.7% [292/362]). ($\chi^2=13.33$, $P<0.001$, $n=381$, 1 df) (Fig. 4). Among equal-sized butterflies in this sample, occupants chased 11 of 13 times (84.6%; $\chi^2=6.23$, $P<0.02$, 1 df).

The difference in outcome between chasing and chased occupants was significantly different for all three years ($\chi^2=14.89$, $P<0.001$, $n=421$, 2 df) and was evident in 1987 and 1988. In 1989, however, there was no significant difference in outcome between chasing and chased occupants ($\chi^2=3.22$, $P=0.20$, $n=84$, 2 df).

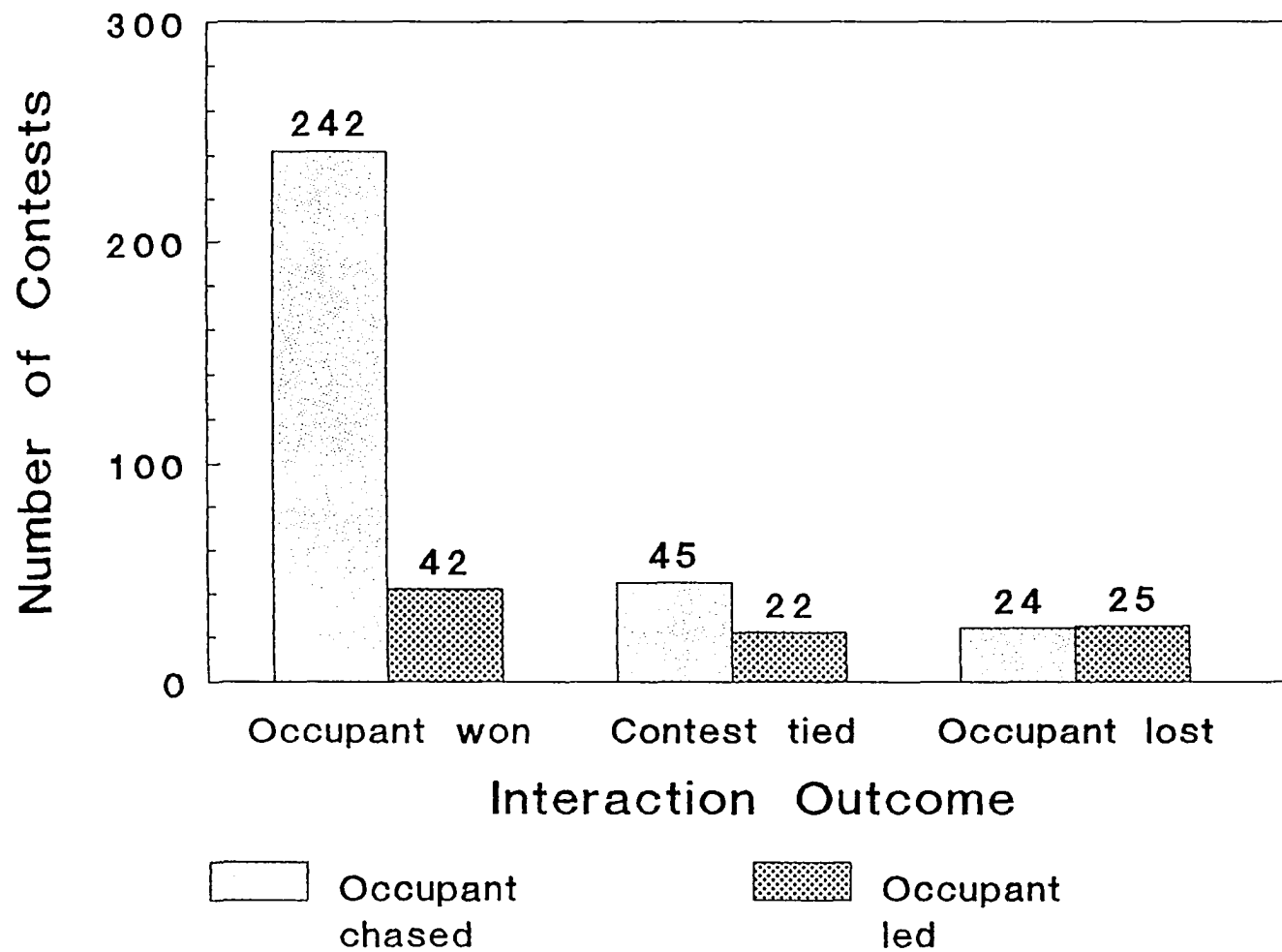
Occupants chasing intruders won more interactions than expected (77.8% [242/311]), while tying or losing in fewer than expected (Fig. 5). Occupants which were chased during interactions won relatively fewer interactions (47.2% [42/89]) and tied or lost more frequently ($\chi^2=36.39$, $P<0.001$, $n=400$, 2 df).

Winning occupants chased intruders in 85.2% [242/284] of interactions, while losers chased only 49.0% of the time [24/49 interactions]. Occupants which tied chased about two-thirds of the time. The above trends were significantly different for all three years and in 1987 and 1988. However, no significant difference in outcome between chasing and chased occupants was found for 1989 ($\chi^2=3.22$, $P=0.20$, $n=84$, 2 df), perhaps due to the relatively small number of interactions observed that year.

Reversals of Chase Position

Contestants reversed position while spiralling in 19 out of 397 interactions, 4.79% of the time. In seven of these reversals, the occupant switched from leading to chasing. Occupants were larger than intruders in 6 out of 7 of these

Figure 5. Interaction outcome vs. occupant's chase position. Numbers of interactions are shown above the bars, which indicate absolute numbers of chasing and leading interactions. Data from the categories "occupant slightly smaller" and "occupant smaller " have been lumped under the heading "smaller." Relative chase positions and outcomes of intruders can also be inferred from the graph: e.g., the number of times which losing occupants led (25) was also the number of times which the winning intruders they had fought had chased. $\chi^2 = 36.92, P < 0.001, n = 421, 2 \text{ df}$.



interactions, and occupants won 5 and tied in two. One of these ties involved the one occupant which was slightly smaller than the intruder. This contrasts with the other 12 interactions in which occupants switched from chasing to leading. Occupants were smaller than intruders in 7 of these chases, slightly smaller in one chase, equal in size in one, and larger in three. These occupants won only four of the 12 interactions, lost 7, and tied once. Of the seven defeated occupants, five were smaller than the intruder, one was slightly smaller, and one was equally sized. Occupants were significantly smaller ($\chi^2=8.25$, $P<0.05$, $n=19$, 3 df) and lost more often ($\chi^2=6.57$, $P<0.05$, 2 df) in chase-to-lead reversals than in lead-to-chase reversals. In chase-to-lead reversals, the distribution of outcomes ($\chi^2=23.56$, $P<0.001$, $n=12$, 2 df) and occupant sizes ($\chi^2=23.62$, $P<0.001$, 4 df) differed significantly (more losses; more smaller occupants) from those of interactions without reversals ($n=378$). In lead-to-chase reversals, however, neither outcomes ($\chi^2=1.40$, $P=0.49$, $n=7$, 2 df) nor size distributions ($\chi^2=5.70$, $P=0.22$, $n=7$, 4 df) differed significantly from those of interactions without reversals.

Interaction Outcome

Excluding interactions for which occupant and intruder could not be differentiated, most interactions (80.1% [431/528]) resulted in clear winners (Fig. 1b). ANCOVA indicates that relative size, chase position and ambient temperature (T_a) affected the outcome of aerial interactions between occupant and intruder males (Table I).

Relative Size and Occupancy

Larger males won 72.3% (337/466) of interactions involving an observable size difference while losing only 9.4% (44/466) ($\chi^2 = 324.11$, $P < 0.0001$, 2 df); the remainder of interactions involved ties between larger and smaller males (18.2% [85/466]) or interactions between males of approximately equal size (13.3% of all 538 interactions [72/538]) (Fig. 1a). The majority (80% [373/466]) of occupants were males larger than the intruders they chased (Fig. 1b); this indicates that size is important in procurement of territorial sites.

Occupants won 83.7% (361/431) of decided contests (Fig. 1b). Since 80% of the larger males involved in interactions were occupants, it is possible that the winning of occupants simply reflects size differences. However, the data also show that occupancy is also significant in determining interaction outcome. Although both larger occupants and larger intruders won more contests than they lost, larger occupants won a significantly greater proportion of decided contests (larger occupants: 94.8% [294/310]; larger intruders: 60.6% [43/71]; $\chi^2 = 66.44$, $P < 0.0001$, 1 df) (Fig. 2). The importance of occupancy is also evident when comparing results between equally sized residents and intruders, and the frequency of wins by smaller residents and smaller intruders. When residents and intruders were equal in size, residents won 39 of 50 (78%) interactions with decided outcomes ($\chi^2 = 15.68$, $P < 0.001$, 1 df). Also, smaller occupants won 28 of 71 (39.4%) of interactions compared to 11 of 256 (4.2%) for smaller intruders ($\chi^2 = 66.44$, $P < 0.0001$, 1 df) (Fig. 2).

Actual Size of Occupants and Intruders

Since *V. atalanta* is migratory, we could not capture previously marked males and determine sizes or weights of actual contestants in interactions. We did sample the occupant and intruder population, however. Occupants were significantly larger and heavier than intruders in both spring and summer broods, and males of the summer brood were significantly larger and heavier than those of the spring brood (ANCOVA, Tables IIA, IIB, IIIA, IIIB).

Interaction Duration

Interaction duration is also significantly affected by relative size, chase position, and air temperature, but not outcome (Table IV). The duration of spiral interactions ranged from 2 to 44 s ($n=397$) with a mean of 11.55 ± 6.35 s and a median of 10.5 s (Fig 6). As size difference decreased, contest duration increased with the longest interactions occurring between equally sized contestants (Fig. 7). Contests in which the occupant was smaller were significantly shorter than those between equally matched contestants ($t=-3.40$, $P=0.0007$) or those in which the occupant was slightly larger ($t=-2.80$, $P=0.0054$). Contests in which the occupant was larger were significantly shorter than those in which the occupant was slightly larger than or equal to the intruder (Table IV). When occupants chased intruders, interactions were significantly shorter but not highly so (Table IV).

Basking time before interactions did not significantly affect interaction duration over the three years of the study, nor did interactions vary in duration over the season. However, when years were considered individually, interaction duration was longer after a longer basking time in 1987 ($F=7.34$, $P=0.0074$,

Table IIA. Correlation of Forewing Length^a with Brood and Status.

Source	df	SS	<i>F</i>	<i>P</i>
Brood	1	5.19	271.43	<0.0001
Status of butterfly	1	0.81	42.44	<0.0001

Brood	Adjusted mean wing length	Wing length difference	Diff. from summer brood? <i>t</i>	<i>P</i>
Spring	2.71 cm	-0.35 cm	-16.48	<0.0001
Summer	3.06 cm	0	-	-

Status of butterfly	Adjusted mean wing length	Wing length difference	Different from occupant? <i>t</i>	<i>P</i>
Vagrant	2.82 cm	-0.14 cm	-6.51	<0.0001
Occupant	2.96 cm	0	-	-

^aMean wing length = 3.13 cm + Brood wing length difference + Status wing length difference. $R^2 = 0.67$, $F = 181.62$, $P < 0.0001$, $n = 178$, 2 treatment df.

Table IIB. Adjusted Mean Forewing Length vs. Status, Within Broods.

Brood	Status of butterfly	<i>n</i>	Adj. mean wing length	W. length difference	Diff. from occupant? <i>t</i>	<i>P</i>
Spring	Vagrant	47	2.65 cm	-0.13 cm	-5.58	<0.0001
Spring	Occupant	35	2.78 cm	0	-	-
Summer	Vagrant	38	2.99 cm	-0.15 cm	-4.27	<0.0001
Summer	Occupant	58	3.14 cm	0	-	-

Table IIIA. Correlation of Live Mass^a with Brood and Status.

Source	df	SS	<i>F</i>	<i>P</i>
Brood	1	0.21	164.30	<0.0001
Status of butterfly	1	0.09	69.12	<0.0001

Brood	Adjusted mean mass	Mass difference	Diff. from summer brood? <i>t</i>	<i>P</i>
Spring	0.162 g	-0.070 g	-12.82	<0.0001
Summer	0.232 g	0	-	-

Status of butterfly	Adjusted mean mass	Mass difference	Different from occupant? <i>t</i>	<i>P</i>
Vagrant	0.175 g	-0.045 g	-8.31	<0.0001
Occupant	0.220 g	0	-	-

^aMean live mass = 0.255 g + Brood mass difference + Status mass difference.
 $R^2 = 0.67$, $F = 181.62$, $P < 0.0001$, $n = 178$, 2 treatment df.

Table IIIB. Adjusted Mean Mass vs. Status, Within Broods.

Brood	Status of butterfly	<i>n</i>	Adj. mean mass	Mass difference	Diff. from occupant? <i>t</i>	<i>P</i>
Spring	Vagrant	47	0.147 g	-0.027 g	-5.29	<0.0001
Spring	Occupant	35	0.175 g	0	-	-
Summer	Vagrant	38	0.200 g	-0.061 g	-6.89	<0.0001
Summer	Occupant	58	0.261 g	0	-	-

Table IV. Correlation of Interaction Duration^a with Relative Size, Interaction Outcome, Chase Position, Ambient Temperature, Resting Time, and Julian Date.

Source	df	SS	<i>F</i>	<i>P</i>
Relative size	4	1039.68	7.08	<0.0001
Interaction outcome	2	62.44	0.85	0.4283
Chase position	1	217.24	5.91	0.0155
Ambient temp. (T_a)	1	226.79	6.17	0.0134
Resting time	1	80.63	2.20	0.1393
Julian Date	1	26.86	0.73	0.3930

Relative size of occupant	Adjusted mean duration	Duration difference	Different from larger? <i>t</i>	<i>P</i>
Smaller	11.50 s	0.07 s	0.06	0.9506
Slightly smaller	13.45 s	2.01 s	1.09	0.2771
Equals intruder	17.94 s	6.51 s	3.70	0.0002
Slightly larger	14.88 s	3.45 s	4.02	<0.0001
Larger	11.43 s	0	-	-

Interaction outcome	Adjusted mean duration	Duration difference	Different from win? <i>t</i>	<i>P</i>
Occupant lost	13.54 s	0.10 s	0.09	0.9288
Contestants tied	14.55 s	1.11 s	1.27	0.2038
Occupant won	13.44 s	0	-	-

Chase position of occupant	Adjusted mean duration	Duration difference	Different from chasing? <i>t</i>	<i>P</i>
Being chased	14.78 s	1.89 s	2.43	0.0155
Chasing	12.90 s	0	-	-

^aInteraction duration = 14.40 s + Relative size duration difference + Chase position duration difference - 0.25 T_a . $R^2 = 0.11$, $F = 4.90$, $P < 0.0001$, $n = 397$, 10 treatment df.

Figure 6. Distribution of contest duration among 397 spiral interactions. Mean duration = 11.54 ± 6.35 s;
median duration = 10.5 s.

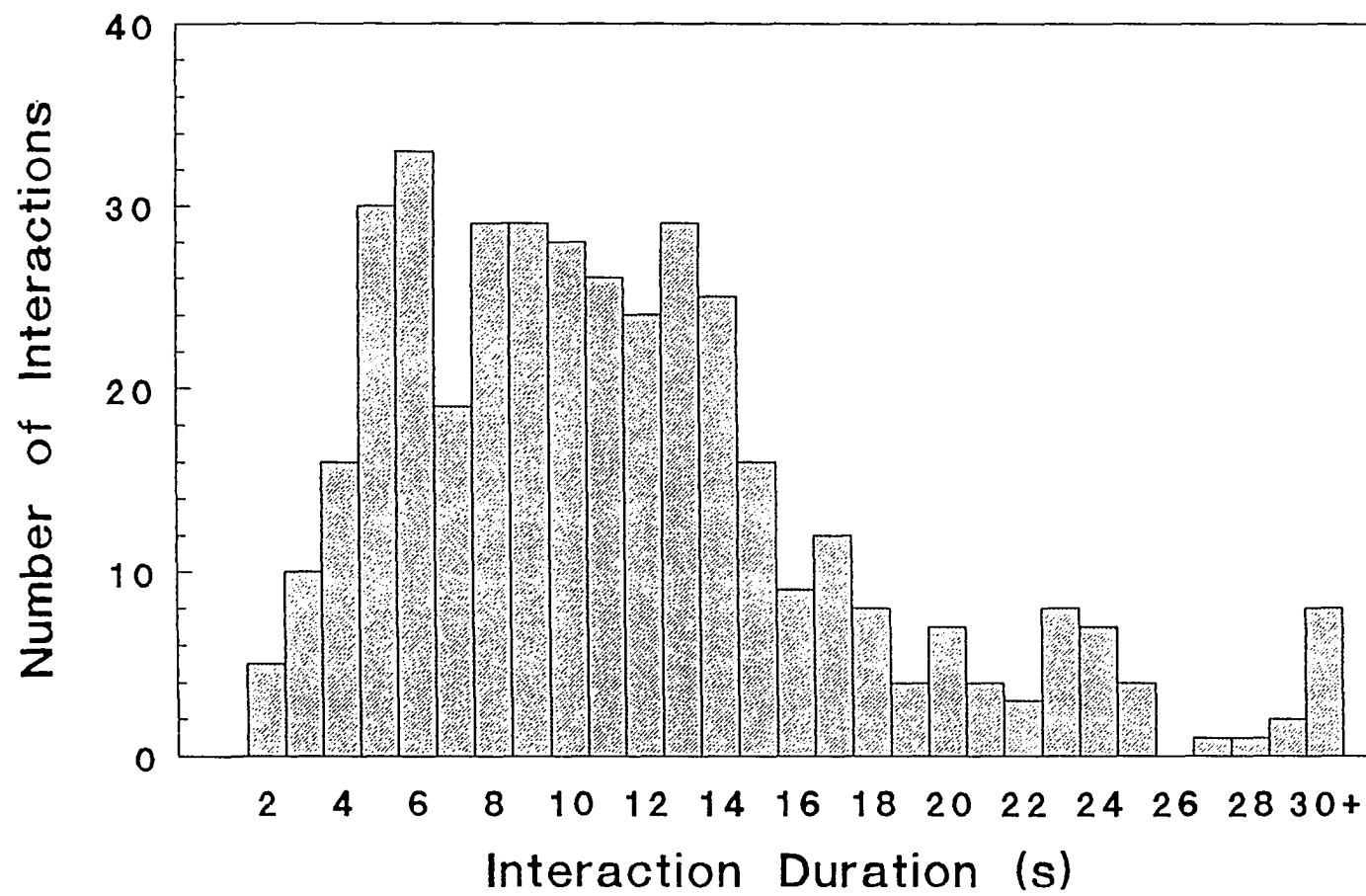
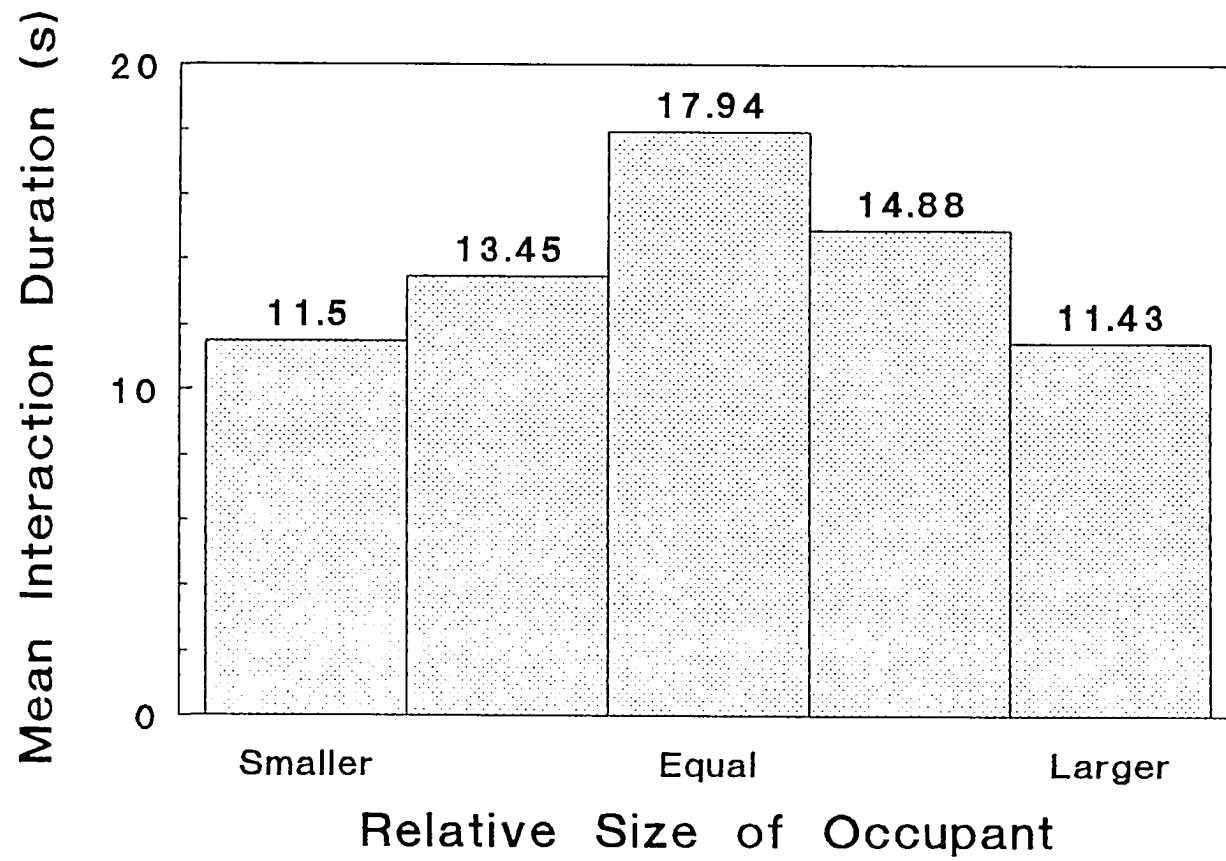


Figure 7. Mean contest duration vs. relative size of occupant. Mean durations in seconds are shown above the bars for each size class. $n = 397$.



$n=197$) and 1989 ($F=8.24$, $P=0.0053$, $n=97$), but not in 1988 ($F=0.16$, $P=0.6904$, $n=85$).

Ambient Temperature

Ambient temperature affected both interaction outcome (Table I) and duration (Table IV). Occupants were less likely to win interactions at higher temperatures; the mean payoff index to occupants (likelihood of winning) decreased by 0.022 units for each 1°C increase (Fig. 8). Interactions were shorter at higher T_a , averaging 0.25 s shorter per °C (Fig. 9).

DISCUSSION

As shown for another nymphalid, *L. weidemeyerii* (Rosenberg & Enquist, 1991), *V. atalanta* males follow the same contest rules as do other territorial animals. These are as follows: 1) larger animals occupy most available territories, 2) occupancy is an advantage regardless of size, and 3) duration of contests decreases as the size difference of combatants increases (Leimar and Enquist, 1984). The results of Rosenberg & Enquist's (1991) study suggest that occupancy is more important for *L. weidemeyerii* than for *V. atalanta*. *L. weidemeyerii* occupants won 90% of their interactions whereas larger males (occupants and intruders) won only 65% of interactions. Also, small residents won 72.2% (13/18) of their interactions.

V. atalanta occupants also won more (82.7%) contests than larger resident and occupant males (72.3%) but the difference between the two values was less. If we would have included short hovering interactions that did not develop into spiral chases, most of the differences in the two sets of data might disappear, since occupants stayed after nearly all of these hoverings. However, contest

Figure 8. Relationship of interaction payoff index to ambient temperature (T_a) for all of 397 interactions.

The three rows of crosses from top to bottom indicate interactions in which the occupant won, tied, and lost, respectively. Payoff index = $3.14 \text{ units} - 0.022T_a$.

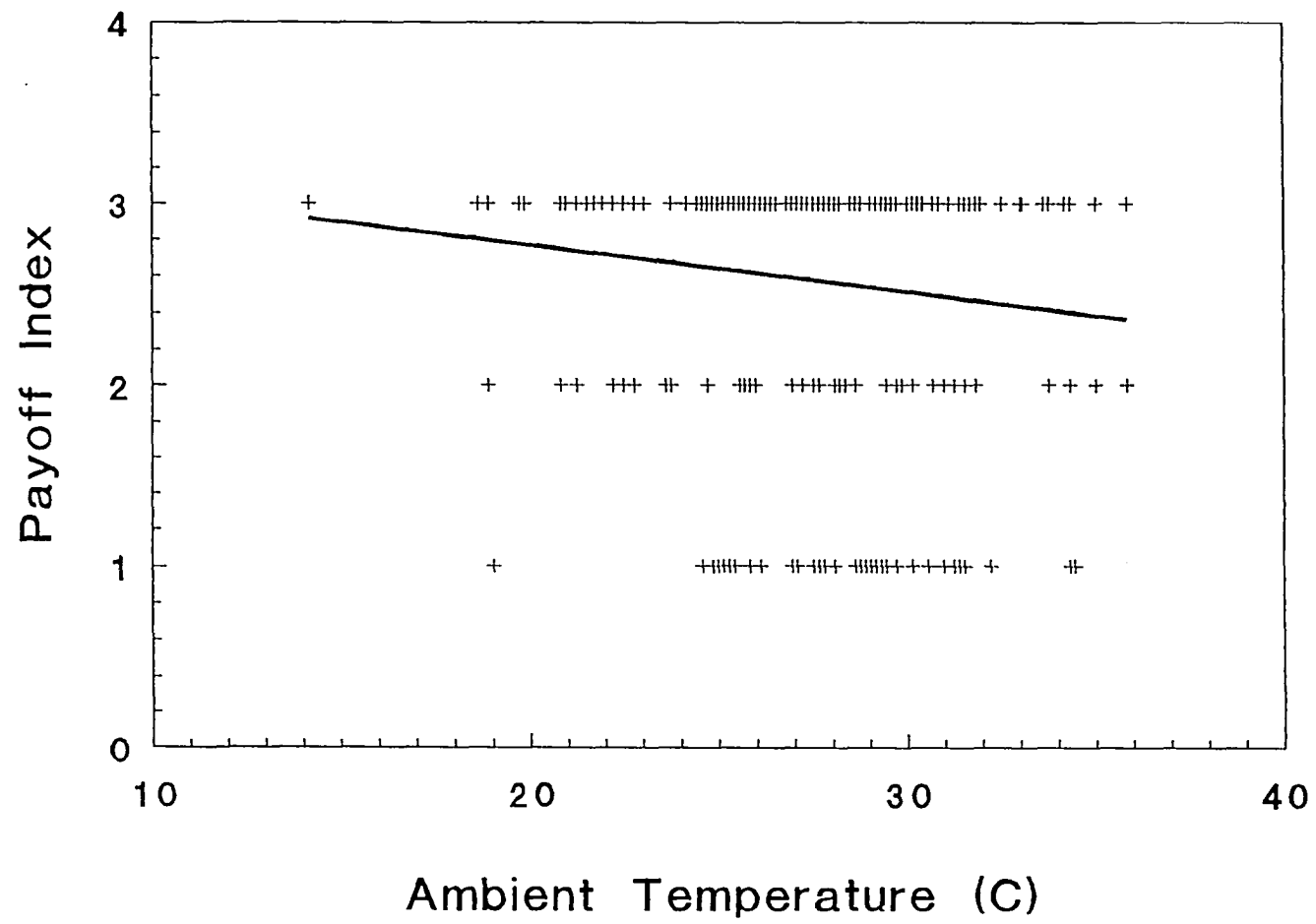


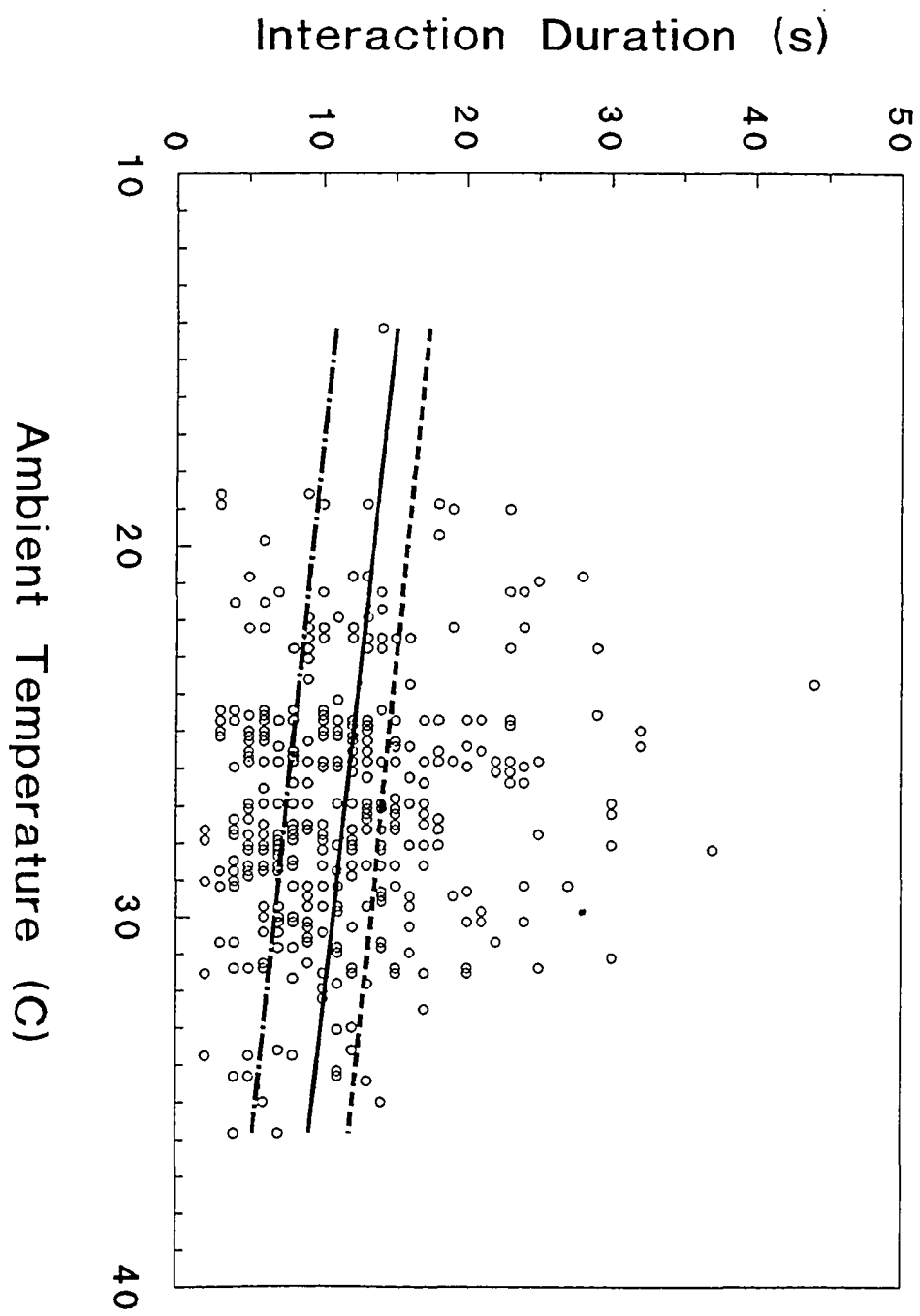
Figure 9. Relationship of ambient temperature (T_a) and relative occupant size to interaction duration.

———— : Regression line for all 397 observations (Duration = 17s.22 - 0.24 T_a).

- - - - - : Duration of interactions when occupants chased and defeated equal-sized

intruders. - . - . - . - : Duration of interactions when occupants chased and defeated smaller

intruders. Duration = 14.40s + Relative size duration difference - 0.25 T_a . $R^2 = 0.11$, $F = 4.90$, $P < 0.0001$, $n = 397$.



outcomes for *V. atalanta* differed most from those for *L. weidemeyerii*, in that smaller *V. atalanta* occupants won only 39.4% (28/71) of their interactions. This difference decreases, however, if non-spiral interactions are included. These latter data may indicate that *V. atalanta* males value mating territories more strongly than do males of *L. weidemeyerii*. A tendency toward a bourgeois strategy (occupant always wins) may occur if the risk of injury is greater and/or the value of the resource is smaller. Davies (1978) gave the latter rationale for a bourgeois strategy in the butterfly *P. aegeria*. Mating territories may not be in short supply for the population of *L. weidemeyerii* which Rosenberg & Enquist (1991) studied. If certain *V. atalanta* territories are much more visually obvious to migrating females (Bitzer & Shaw, 1979), then these prime territories may be important enough for *V. atalanta* males to contest. The mean duration of interactions might then be longer, or the proportion of spiral interactions higher, in optimal territories than in suboptimal ones which are off the main flight routes.

Larger *V. atalanta* males won 72.3% of decided contests while losing only 9.4%. Larger males may be physically stronger or more maneuverable, and size is very likely a cue by which males can resolve contests with minimum risk of injury. Interactions also shortened as size differences between contestants increased. These findings suggest that spiral flights are true contests in which asymmetries in RHP other than prior occupancy are important.

The importance of body size in *V. atalanta* interactions contrasts with that of *Papilio polyxenes* in which an occupant's wing length is irrelevant to its success in defending a territory (Lederhouse, 1982). Prior occupancy and the number of competitors already present, rather than size, determine interaction

outcome in this long-winged, slow-flying species. Nymphalids such as *Inachis io* and *Aglaia urticae* (Baker, 1972) and *V. atalanta* are shorter-winged, faster-flying species and may be better able to take advantage of their size in aerial interactions.

Rosenberg & Enquist (1991) do not consider when butterfly contests are decided. Since nearly all *V. atalanta*, and probably *L. weidemeyerii*, occupants win interactions of 3 s or less (i.e., interactions which do not develop into spiral chases), contest decisions are probably made during one or several successive chases. Outcome of interactions is significantly related to the occupant's position in the spiral interaction. Occupants which won interactions chased the intruders more frequently than did occupants which tied or lost. When we observed bouts of several interactions during which the intruder defeated the occupant, the occupant chased in the initial interactions and was chased in the final interaction(s). The occasional reversals during single spiral interactions also showed that chasing is the better position. Occupants which switched from being chased to chasing recovered a dominant position and frequently went on to win the interaction, whereas those which switched from chasing to leading were often defeated. Reversal type was also related to relative size of occupant and intruder. Occupants switching from leading to chasing were nearly always larger, whereas those switching from chasing to leading were much more often smaller.

Occupancy, however, was more important than chase position in determining outcome; only 28% of intruders that chased displaced the occupant. Nevertheless, an intruder may win by persisting through several interactions. Baker (1972) showed that during the first two interactions after the intruder

arrives, the original occupant is more likely to return and repitch in the territory than the intruder. From the third interaction onwards, however, they are more or less equally likely to return and repitch. Baker (1972) suggests that the intruder quickly learns the area surrounding the territory and can more easily find its way back.

Although *V. atalanta* males occasionally reverse positions while spiralling, most chase positions are decided during the circling and hovering of the initial encounter prior to the spiral chase. Baker (1972) referred to this initial circling as the two males jockeying for position with each butterfly trying to get above and behind the other. Rosenberg and Enquist (1991) make the point that interacting butterflies may gradually obtain information about each other's fighting ability. However, they do not indicate how they might do so, such as during a spiral interaction or series of spiral interactions.

Previous analyses of interactions between occupants and intruders of a number of territorial species have shown that as contestant size differences increase, contest duration decreases. This has now been shown for two butterfly species, *L. weidemeyerii* (Rosenberg & Enquist, 1991) and *V. atalanta*. In this study we were surprised to find that, even though larger males won more often and interactions were shorter when size difference was greater, interaction duration itself was not significantly correlated with outcome. Wickman and Wiklund (1983) hypothesized that longer interactions during cooler weather indicate that both occupants and intruders fight harder over territories. The net effect this dynamic suggests is that occupants are roughly equally likely to retain their territories whatever the T_a . We nevertheless found a slight tendency for occupants to lose interactions more frequently on warmer days for

reasons perhaps unrelated to duration. Baker (1972) likewise found that for *I. io*, the mean interaction duration on the relatively few occasions that the intruder did return to the territory after being intercepted (corresponding to ties or losses for *V. atalanta* occupants) was not significantly different from the interaction duration when the intruder did not return (corresponding to wins by occupants). Nevertheless, during the longer interactions, if the occupant drove the intruder farther from the territory, the intruder was less likely to return. For *I. io*, the distance an occupant drives an intruder away from its territory may be more important than the amount of time it spends doing so, although both factors are somewhat correlated. The role of occupancy in *V. atalanta* might also explain the failure of interaction duration and outcome to be correlated, i.e., the tendency for small occupants to win shorter bouts with larger intruders. Another factor which needs to be considered in our study is whether intruders do better after persisting through several interactions with a single occupant, as Baker (1972) demonstrated.

Median contest duration was longer for *V. atalanta* (10.5 s) than for *L. weidemeyerii* (6 s; Rosenberg and Enquist, 1991), although mean durations were similar for both species (11.55 s and 11.1 s, respectively). Contest duration is thus more normally distributed for *V. atalanta* than for *L. weidemeyerii*, for which the distribution appears to be negative binomial. Several possible explanations come to mind. One reason that *V. atalanta* durations may be more normally distributed is that our analysis excluded many shorter hovering and horizontal interactions which never developed into spiral contests. However, Rosenberg and Enquist's (1991) sample of 157 interactions likewise seems to be a subsample of true contests among the total of 502 interactions. Therefore,

another reason for this difference may be that *V. atalanta* contests are multi-step sequences in which hovering and horizontal chasing precede spiraling. Once either occupant or intruder decide to go beyond hovering, the contestants may need a certain amount of time to jockey for position before beginning to spiral. This requirement should tend to eliminate very short spiral contests. We thus further speculate that samples including both spiral and non-spiral interactions might include a duration distribution which is bimodal to some extent.

Baker (1972) found that only 6% of *I. io* males arriving at an already occupied territory eventually ended up occupying it. This compares with our own findings that occupants win ca. 95% of their interactions [including both spiral and non-spiral interactions (unpublished observations)]. The size and weight differences between *V. atalanta* broods introduce another factor which complicates the question of occupancy. Unlike *I. io*, which is single-brooded in Great Britain (Baker, 1972), *V. atalanta* is double-brooded in Iowa, and both summer brood occupants and vagrants are larger than spring brood occupants (Tables IIB, IIIB). When larger, younger summer-brood males appear abruptly in mid-June, they seem to quickly displace the remaining spring brood males (unpublished observations). We have occasionally observed surviving, weathered spring brood males adopting a stealth strategy by perching quietly in the outer fringes of territories held by summer brood males (unpublished observations).

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GENERAL DISCUSSION

Daily Schedule, Climate Space, and Duration of Daily Territorial Period

Since butterflies are ectotherms which rely partly upon solar radiation or other external heat sources to stay warm enough to fly vigorously, it is hardly surprising that they often opportunistically combine mate-locating and thermoregulatory strategies (Douwes, 1976; Shreeve, 1984; Dennis and Shreeve, 1988; Rutowski *et al.*, 1994; Bitzer and Shaw, 1995). Mating strategy in some species changes as both climatic and biological factors vary (Wickman and Wiklund, 1983; Wickman, 1985a; 1985b; 1988; Rutowski, 1991). Since climatic factors are often predictable over the course of the day, then so might be the periods when male butterflies of various species either patrol large areas in search of receptive females, or alternately, adopt a more stationary strategy such as perching or defending territories.

The mode of mate-location is related to diel and seasonal activity patterns and habitat use (Dennis, 1993, p. 33). Perching and territorial species can adjust the timing of their mate location strategies according to the weather, climate, and population structure. There are thus two groups of factors which affect whether or when butterfly males of the same or different species perch or patrol: 1) climatic factors which affect body temperature and 2) demographic factors such as male or receptive female population density and distribution (Dennis and Williams, 1987; Rutowski, 1991; Scott, 1974; Wickman and Wiklund, 1983; Wickman, 1985a; 1985b; 1988). Different species of perching butterflies seem to follow daily activity schedules which are primarily climate-dependent, or primarily density-dependent, or both. There may also be an

interaction between climatic conditions such as higher ambient temperature (T_a) and higher vagrant male density which reduce the benefits of holding a territory at higher T_a (Wickman and Wiklund, 1983). Territoriality thus declines and patrolling increases with higher T_a for *Pararge aegeria* (Wickman and Wiklund, 1983), *Coenonympha pamphilus* (Wickman, 1985a), and *Lasiommata megera* (Dennis, 1982). The territorial period of the hesperiid *Ochlodes venata* seems to have both climate- and density-dependent features. On sunny days, *O. venata* patrols during the mornings and is territorial during the afternoons, while on cloudy days it patrols in the afternoons, probably in response to a higher density of females which have remained unmated due to unfavorable thermal conditions in the morning (Dennis and Williams, 1987).

Some perching and territorial species do not seem to start territorial activity at well-defined periods of the day. Instead, the ratio of perching to patrolling males shifts over the course of the day. Although this ratio is highest during times (before mid-morning and after mid-afternoon) when conditions are thermally most favorable for perching, a few individuals continue to perch even during mid-day. In the satyrids *Pararge aegeria* and *Coenonympha pamphilus*, for example, males patrol for females at warmer temperatures and defend sunlit patches at lower temperatures while waiting for females to alight and bask (Wickman and Wiklund, 1983; Shreeve, 1984; Wickman, 1985a). These satyrids move from sun patch to sun patch and the period during which they defend sunlit patches varies with the change in air temperature.

Other territorial species, such as *Aglais urticae* and *Inachis io* (Baker, 1972), *Vanessa atalanta* (Bitzer and Shaw, 1979; Swanson, 1979; personal communication), and *Lasiommata megera* (Dennis, 1982) start territorial

activity at more predictable times. Males establish territories in predictable areas, apparently defined by certain visual features, at a specified time and duration each day. In these species, males may fly up from perches or from intermittent patrols within their territories to intercept females flying through the territories. Like zeitgebers of biological rhythms, climatic factors apparently modulate when such territorial behavior begins and ends. Mid-day onset of territorial behavior in some species may be related to attenuation of polarized light in the zenith during that period (Fitzpatrick and Wellington, 1983). For example, *Limenitis lorquini* males return to their territories each day just before solar noon and remain there as long as the midsummer sun's aureole disrupts zenith polarization. If the sky is overcast, they do not come (Wellington, 1974). Territorial start times of *Vanessa atalanta* males may likewise depend partly upon sky polarization patterns. When there is broken overcast with small patches of blue sky visible, *V. atalanta* males start territorial activity at the same times as they do on clear days, but under solid overcast, they start ca. 0.5 - 1.0 h later.

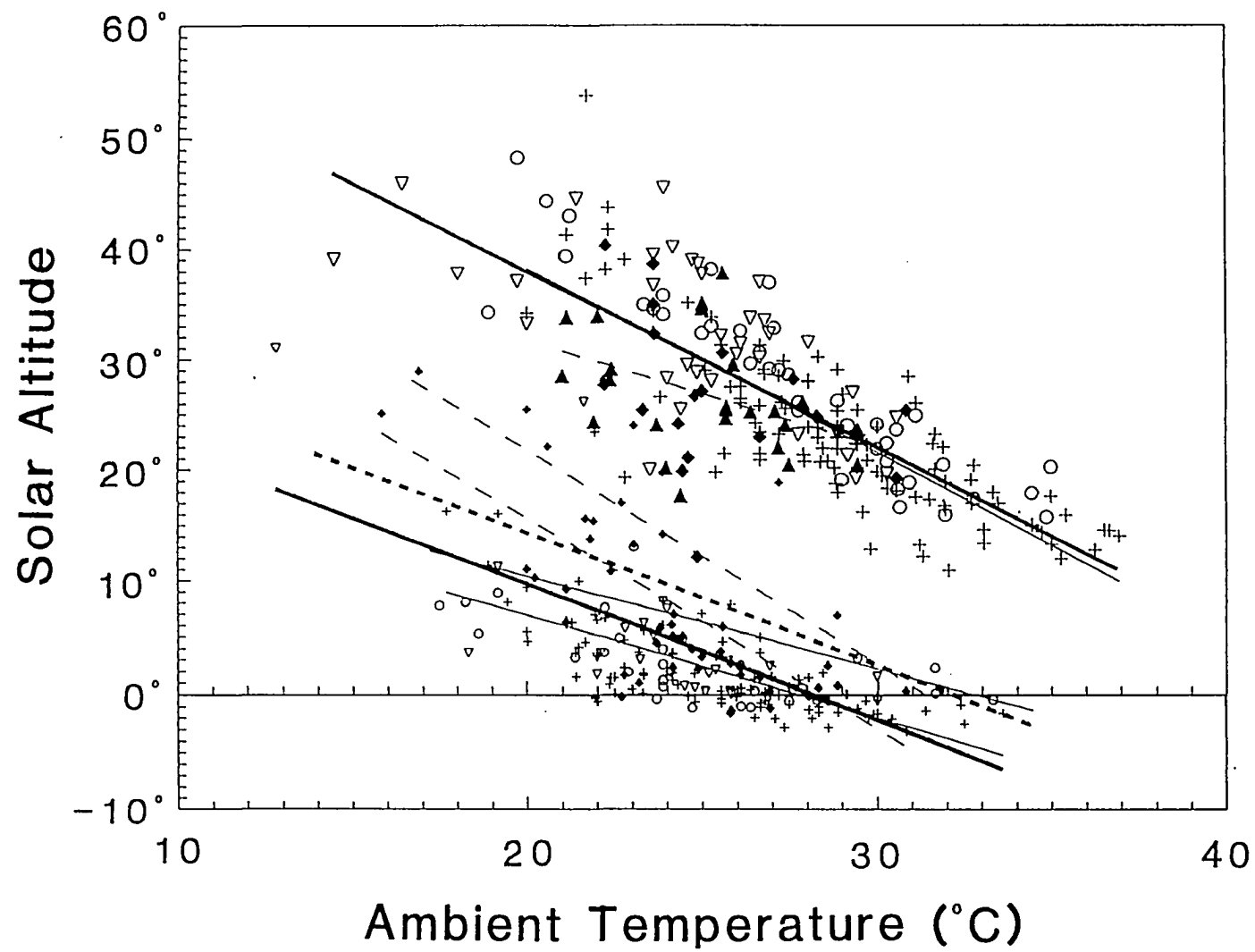
Although the nymphalid *Argynnis paphia* is a patrolling species which is non-territorial, its response to climatic conditions is similar to that of perching and territorial butterflies with well-defined arrival times. It thus provides a basic model for understanding the conditions which define the territorial period of *V. atalanta* males. *A. paphia* stops flying and starts basking whenever climatic conditions result in body temperatures too low to maintain flight. Vielmetter (1958) described a "change of state" in which the non-territorial nymphalid *Argynnis paphia* switched between continuous flight and stationary basking according to an inverse relationship between ambient temperature (T_a)

and solar radiation (R_{\odot}). When the air temperature was low, males flew only when the sun, and therefore R_{\odot} , was high. On warm days, males could fly longer and not need to perch until the sun was low in the sky. Various combinations of these two factors yielded a critical body temperature (T_b) of 34.2°C , at which butterflies would switch from one behavior to another. *A. paphia* likewise decamps from its perch at a lower critical T_b of 23.4°C and flies up into nearby trees (*Baumflug*) to roost for the night (Vielmetter, 1958).

A similar relationship was found for *V. atalanta* start time on sunny days (Bitzer and Shaw, 1995). *Vanessa atalanta* males take advantage of climatic factors in this way by establishing territories during late afternoons. Late afternoon is a period when butterflies can still fly, but the weather is becoming too cool for them to do so continuously without stopping to rest and bask in the sunshine at intervals to rewarm themselves. Territorial *V. atalanta* males take advantage of this period by switching abruptly to stationary perching and basking for the rest of the afternoon. Such basking may allow them to maintain optimal body temperatures at a lower metabolic cost than by patrolling (Alcock, 1985), and thus to keep themselves warmer and more maneuverable than the incoming intruders which challenge them.

The first three chapters in this dissertation show that the daily territorial period of *V. atalanta*, lasting for a period varying from ca. 1.5 to 3.2 h from mid- to late afternoon until near sunset, is defined by climatic transition boundaries in which the butterflies switch from one type of behavior to another. We have identified three critical transitions in *V. atalanta* territorial behavior which correlate with particular combinations of solar radiation and ambient temperature, namely 1) *start time*; 2) *end dance*, and 3) *end time*. Figure 1

Figure 1. Relationship of ambient temperature (T_a) to start time and end time (expressed as the corresponding solar altitude), by cloud cover. Sky conditions: + : Clear sky; O: Cirroform cloudiness; ∇: Cumuliform cloudiness; ◆: Broken overcast; ▲: Solid overcast. Larger symbols denote start time solar altitudes; smaller ones, end time solar altitudes. — : Upper line: Regression line for all 214 observations at start time ($STSA = 69°.94 - 1.60 T_a$). Lower line: Regression line for all 198 observations at end time ($ETSA = 33°.84 - 1.20 T_a$). Heavy - - - - - : Regression line for all 198 observations at end dance ($EDSA = 38°.22 - 1.19 T_a$). — : Regression lines for clear skies: Upper line: $STSA = 71°.82 - 1.67 T_a$. Middle line for end dance solar altitude: $EDSA = 26°.83 - 0.82 T_a$. Lower line: $ETSA = 24°.98 - 0.90 T_a$. - - - - - : Regression lines for overcast skies: Upper line: $STSA = 50°.86 - 0.96 T_a$. Middle line: $EDSA = 60°.10 - 1.91 T_a$. Lower line: $ETSA = 53°.37 - 1.87 T_a$. $EDSA = 38°.22 - 1.19 T_a$.

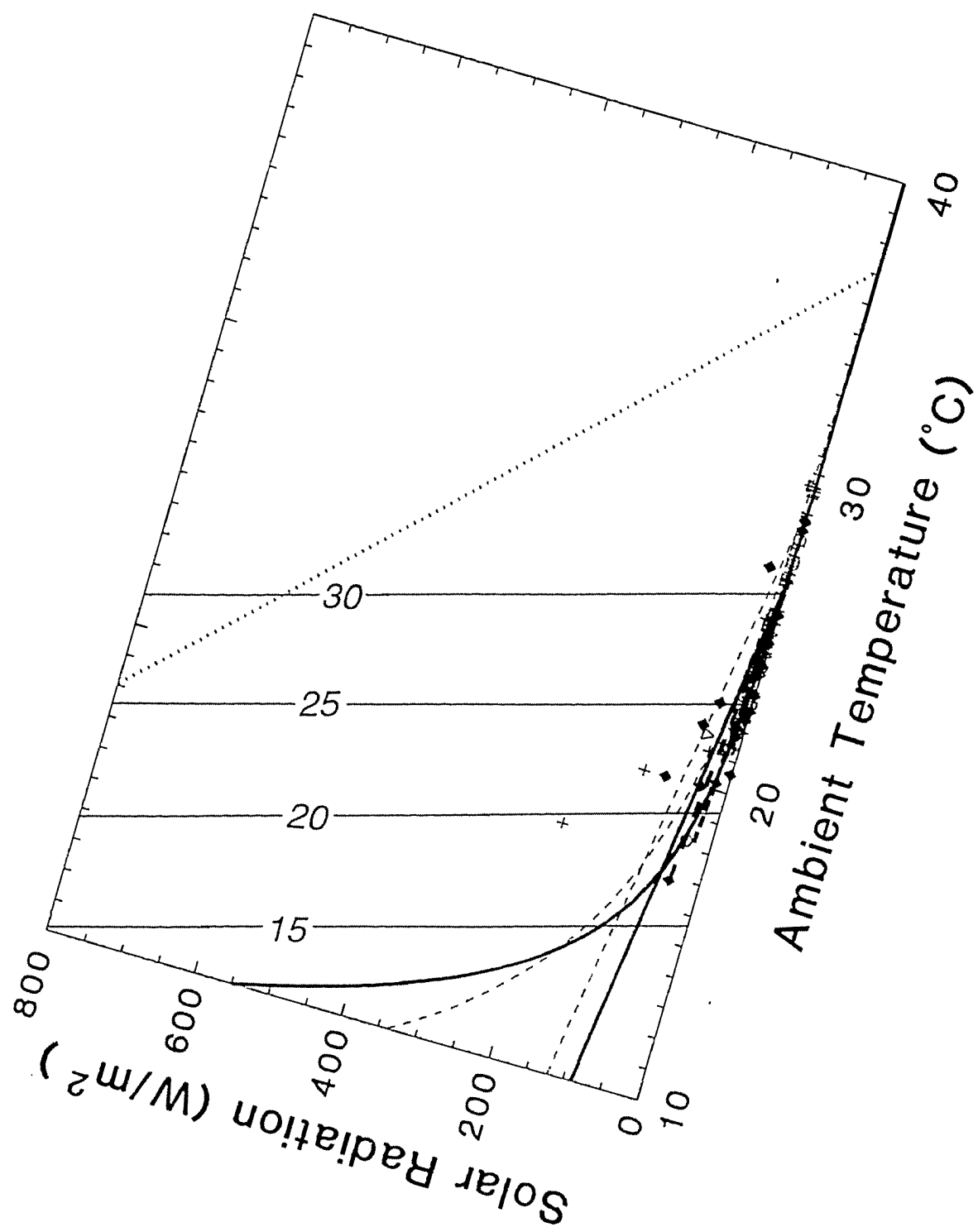


shows these three boundaries as well as the region of solar altitude and T_a within which *V. atalanta* males maintain territories. Figure 2 shows the corresponding solar radiation levels and thus depicts the climate space for *V. atalanta* territorial behavior. Since only variations in end dance time, and not in start time or end time, were correlated with wind velocity (V_w), the upper and lower boundaries of the climate space do not vary with V_w .

The daily activity schedule of *V. atalanta* males depends mainly upon the variation of ambient temperature and solar radiation throughout the day. *V. atalanta* males fly down from their roost sites in tree branches during mid-morning (ca. 0830-0930 h), and bask on sunlit ground or on tree trunks to prepare themselves for flight. Once they have attained a sufficiently high body temperature, they commence feeding and daily migration. They often continue to feed and move about throughout mid-day. Staying warm enough to fly is not then a problem for *V. atalanta*, because the sun is high in the sky and radiational heat is readily available. *V. atalanta* males then can, and often do, fly for long periods of time without needing to bask. [On the hottest days, however, there might be a period when butterflies can overheat in flight, so they may be forced to remain inactive in shade for a while (Vielmetter, 1958) until the weather starts to cool again later in the day.]

As the afternoon passes, the sun drops lower and lower in the sky, and the available solar radiation continually decreases. At some point during the day, the radiation decreases to a critical level at which *V. atalanta* can no longer maintain its optimal body temperature while flying continuously. When this happens, the Red Admiral flies downward to a sunny spot on the ground to

Figure 2. Correlation of ambient temperature (T_a) and solar radiation (R_{\odot}) at start time on 62 days, and at end dance time and end time on 94 days. Sky conditions are indicated as in Fig. 1. Sloping solid contour lines are isotherms of equilibrium body temperature (T_b) of freshly-killed *V. atalanta* males at rest on the ground with wings folded and parallel to the sunlight, recorded at 1-min intervals during the territorial period on 6 days in 1992 ($n = 577$). After locating T_a and R_{\odot} on the axes, read the predicted T_b from the diagonal isotherm contours. *V. atalanta* end time: _____ : Clear sky, linear: $R_{\odot} = 141.73 \text{ W/m}^2 - 5.20T_a$. Clear sky, exponential: $R_{\odot} = 14,817.9e^{-0.329T_a}$. *V. atalanta* end dance time: - - - - - : Clear sky, linear: $R_{\odot} = 184.07 \text{ W/m}^2 - 6.18T_a$. Clear sky, exponential: $R_{\odot} = 2606.64e^{-0.204T_a}$. T_b with closed wings $= 0.0096 R_{\odot} + 1.38 T_{a75 \text{ cm}} - 6.55^{\circ}$: R_{\odot} vs. T_a at start time on sunny days: $R_{\odot} = 1557.46 \text{ W/m}^2 - 41.94 T_a$.



rewarm itself. If it then shows signs of having claimed the site, say by patrolling the area or chasing an incoming intruder, this is the territorial *start time*. On warmer days ($T_a > 30^\circ\text{C}$), *V. atalanta* males need only rest on the ground with wings closed to rewarm, but on cooler days, they bask dorsally in sunlight to varying degrees. Since the ground and the air just above the ground is warmer than the 1 to 2 meter level at which *V. atalanta* typically flies, the butterflies can still stay warm enough by resting or basking so that they can vigorously chase incoming intruders. Thus *V. atalanta* males begin to use the later part of the afternoon for territorial behavior. Start time is delayed 0.5 to 1.0 h on overcast days, perhaps because of low R_{\odot} levels, loss of solar altitude cues, or lower substrate temperatures (Bitzer and Shaw, 1995), or a slower decline in the number of receptive females mated earlier in the day by patrolling males (Dennis and Williams, 1987; Iwasa and Obara, 1989).

As the territorial period gets underway and solar radiation levels continue to decrease, the frequency of intruders rises over the next 1.5 to 2.0 h, peaks, and then declines more quickly than it rose (Bitzer and Shaw, 1979).

Eventually the last intruder of the day flies through the territory and interacts with the occupant. This is the *end dance* (Bitzer and Shaw, in preparation). The end dance estimates when intruders have cooled to an intermediate critical T_b at which *V. atalanta* males can fly within but not between territories. When the environment cools to this point, intruders cease entering occupied territories and any subsequent territorial interactions occur between joint occupants. On warmer days, however, vagrant males seem to stop flying in response to oncoming darkness before the T_a drops low enough for T_b to drop to this critical level. End dance, unlike start time, occurs earlier when

V_w is higher, probably because flying butterflies are more susceptible to convective cooling by the wind than are perched ones. It also occurs earlier on overcast days because it is more R_{\odot} -dependent than is start time. Since R_{\odot} declines to comparable levels earlier on overcast afternoons, end dance time is correspondingly earlier. Since on overcast days, start time is later and end dance time is earlier than on non-overcast days, the active part of the territorial period is then reduced in length (Fig. 1).

After end dance comes the final portion of the territorial period, the *waiting time*, the period during which a *V. atalanta* male stays in its territory after end dance. One might expect it to be advantageous for *V. atalanta* males to leave their territories as soon after end dance time as possible. End dance time, however, is quite variable due to the above-mentioned secondary climatic factors, and because end times tend to occur later on days when the interaction frequency has been higher. If receptive females come only rarely to male territories, it may pay for the male to wait in his territory for a certain length of time in hopes that a late-arriving female might enter it.

The final transition, *end time*, is the moment when the occupant decamps and flies off to roost. Although correlated with T_a and R_{\odot} as is the corresponding *Baumflug* of Vielmetter (1958), it is difficult to say to what extent end time depends directly upon climatic factors. Since the waiting time between end dance and end time remains constant over the entire range of cloud cover and under non-overcast sky conditions, the time at which occupants leave could depend primarily upon this interval.

Although the basic $T_a - R_{\odot}$ dependent model of climate-dependent perching and flight activity periods of butterflies and other insects throughout

the day has been described and explained to varying degrees by a number of investigators (Vielmetter, 1958; Shields, 1967; Douwes, 1976; Swanson, 1979; Shreeve, 1984; Alcock, 1985; Alcock and O'Neill, 1986; Wickman, 1985a; 1988; Gaugler and Schutz, 1989; Brown and Alcock, 1991; Rutowski, 1991), we have examined and modeled what occurs at the transitions of start time, end dance, and end time in more detail. We have also studied some of the additional climatic and behavioral factors which complicate the basic transitions defined by ambient temperature and solar radiation. By also describing the events of the daily activity schedule in terms of solar altitude, we have shown how to compare the activity schedule of *V. atalanta* in Iowa with those of other populations and species in different geographical locations.

As do start time (Swanson, 1979; Swanson and Bitzer, in preparation; Bitzer and Shaw, 1995), end dance time (Bitzer and Shaw, in preparation), and end time (Bitzer and Shaw, in preparation), the daily activity schedule itself varies with solar declination, with the latest event times occurring toward mid-summer. Brown and Alcock (1991) have likewise shown that arrival and departure times of *Vanessa* sp. vary with the seasons.

V. atalanta males both arrive at and depart their territories earlier on cooler days. Although they may tend to keep their territorial period constant, it nevertheless becomes shorter on warmer days. This may occur because on warmer days, butterflies may leave in response to oncoming darkness rather than to temperature, which may still be high enough for them to remain active.

According to Dennis and Shreeve (1988), there are probably few, if any, species of butterflies which adopt perching as their sole mating strategy. The nymphalid *Aglais urticae* may be one such species. It is possible that since *A.*

urticae mates only when it goes to roost after a period of perching (Baker, 1972; Mikkola, 1976; but see Scott, 1974), it may never patrol for mates before its territorial period. Butterflies with similar habits would be most likely to have the strongly climate-dependent start time characteristic of *Vanessa atalanta*. Since courtship occurs only after the territorial period is underway, the number of receptive females does not decrease during the course of the day, and therefore should have no effect upon when males begin perching. This contrasts with species such as the hesperiid *Ochlodes venata* (Dennis and Williams, 1987) in which diurnal switches from patrolling to perching depend upon the density of receptive females. *O. venata* males patrol in the mornings when receptive female density is high, and begin perching as female density drops off in the afternoons. During days with cloudy mornings, males patrol in the afternoons as receptive female density has not been reduced in the mornings (Dennis and Williams, 1987). Later start times of *V. atalanta* on cloudy days might likewise be explained by delayed reduction of receptive female density, were it not for the fact that start times run earlier on cooler days under overcast as they do on other days. Cooler weather should likewise delay reduction of receptive female density and cause start time to be later (Iwasa and Obara, 1989). Yet this does not occur with *V. atalanta* (Bitzer and Shaw, 1995).

The combined evidence indicates that *V. atalanta* males' decisions to both start and end territorial activity for the day are thus more complex than the simple "change of state" responses which Vielmetter (1958) describes.

Habitat Variation and Intra- and Interspecific Differences in Daily Schedule and Territorial Behavior

Whether or not a butterfly starts territorial behavior at a predictable time may also depend upon its habitat, as will the relative importance of T_a , T_s , R_{\odot} , and V_w . Moderately high T_b on sunny days and the small V_w and great R_{\odot} effects upon T_s indicate that *V. atalanta* perch sites are thermally optimal at start time on sunny days as well as usually protected from rapid microclimate fluctuations.

Lasiommata megera (Satyridae) males perch on rocky, sparsely-vegetated hilltops most of the day and move around or up or down the hill as the sun's azimuth, T_a , T_s , V_w , etc. change (Wickman, 1988). *L. megera* males can choose sites of various slopes and sun exposures and thus need not be tied to a particular climatic schedule. T_s and near-ground T_a are often excessive at these sites, as is V_w , which affects both these factors much more strongly than upon flat ground (Wickman, 1988). *V. atalanta*, in contrast, uses patchily-lit but well-sheltered spots on flatter ground and so must wait for the sun to move to a particular altitude. Overly high T_s is rare in *V. atalanta* territories; males can avoid sunspots anyway by moving to shade, as does the nymphalid butterfly *Asterocampa leilia* (Rutowski *et al.*, 1991). Only on days when T_a was above 33°C at start time did *V. atalanta* males ever reject a sunlit territory and go to a shady one. *A. leilia* in open, arid sites in central Arizona escape hot ground by moving onto vegetation (Rutowski *et al.*, 1991). Although *V. atalanta* never escaped high T_s this way, we have seen them reperch on sunlit branches 4 m up soon after arrival on 5 sunny days when T_s was unusually low (< 30°C).

Butterflies living beneath forest canopy (Davies, 1978; Shreeve, 1984) often fly through shade, and so should perch frequently in sun patches throughout the

day. The nymphalid butterfly *Polygonia comma*, a forest species occupying sun patches during midafternoon, follows these as they move and has no predictable start time (unpublished data). *P. comma* leaves territories more predictably later in the afternoon as the sunlight becomes too weak to keep them warm.

Different *V. atalanta* populations may vary in the extent to which start time is climate-dependent vs. density-dependent. According to Swanson and Bitzer (in preparation), start times of *V. atalanta* males in north-central Florida are less predictable by T_a than are those of Iowa *V. atalanta* males. Florida *V. atalanta* males also start earlier on days when interaction frequency during the territorial period later becomes higher. These data suggest that *V. atalanta* start time is more density-dependent in Florida and support Iwasa and Obara's (1989) game theory model for mating strategy in male butterflies.

Contest Dynamics

One reason that territorial behavior was slow to be recognized and studied in insects was that physical aggression in defense of resources is often less overt than it is for birds and mammals (Baker, 1983). Butterflies especially seem to have little capacity for physical aggression. Thus Scott (1974) and Suzuki (1976) maintained that what seemed to be a perching male butterfly's "defense" of an area could alternatively be interpreted as the male's merely investigating passers-by to determine their species and sex. Intruders' so-called "evasive" response could likewise be interpreted as an attempt to avoid a possible predator (Scott, 1974).

Baker (1983) argued that an animal can defend a resource without once showing overt physical aggression. If we observe that whenever an individual

occupies an area, every intruder into that area moves on rather than remaining. Suppose we then remove the occupant and find that the area is invariably occupied quickly by one of the first intruders to arrive. This observation alone is enough for us to conclude that a territorial system is operating, he maintains, even if we never saw contact between occupant and intruder. Among insects, such removal experiments, Baker (1983) claims, have been one of the primary means of demonstrating territoriality (Baker, 1972; Davies, 1978).

A stronger argument for true territoriality among butterflies is to show that the distribution of outcomes of interactions between occupants and vagrants do follow patterns which game models predict should occur if true contests are occurring. These predictions are as follows: 1) larger and/or stronger butterflies should occupy and accumulate in territories; 2) the greater the differences in size and strength between contestants, the shorter the contest (Enquist and Leimar, 1983), and 3) given animals of equal size, occupants should win more contests than intruders (Maynard Smith and Parker, 1976; Leimar and Enquist, 1984).

Such evidence for true territoriality has been found for several butterfly species. Wickman (1985) showed that resident *Coenonympha pamphilus* males were larger on average than intruders. Rosenberg and Enquist (1991) demonstrated that larger *Limenitis weidemeyerii* males were more successful in both defending and capturing territories, and, when size differences were taken into account, occupants were more successful than intruders. One effect of such competition is that larger males should tend to accumulate in territories over time; this is, in fact, what Rosenberg and Enquist (1991) and Bitzer and Shaw (in preparation) have found.

Further proposed investigations include analysing the existing data by partitioning it by groups such as winners or losers, or butterflies of a particular relative size. Some analyses performed just before this dissertation was completed suggest, for example, that the difference in interaction duration between chasing and chased occupants was greatest (8 vs. 15 s) when the occupants were relatively much smaller than the intruders, whereas when the occupants were much larger, duration differences between chasing and chased occupants were insignificant. Why this might be so has yet to be explained.

Temperature-induced asymmetry between conditions experienced by occupants and intruders might explain part of the advantage of being an occupant. Since temperature differences between the warmer perching substrate and the cooler air flight level are greater on cooler days ($\Delta T \geq 20^\circ\text{C}$) and less on warmer days ($\Delta T \leq 5^\circ\text{C}$), this might partly explain why occupants are somewhat more likely to retain territories on cooler days (Bitzer and Shaw, in preparation). If temperature differences explained a substantial part of the advantage of occupancy, however, we would expect this advantage to diminish greatly on overcast days as well as later in the territorial period on sunny and partly cloudy days as the sun drops lower in the sky and substrate temperature decreases. Some experimental procedures such as providing an artificially-warmed perching substrate such as a light-colored heating pad to see whether interaction durations or occupants' payoff indices might increase as a result might also provide some additional answers to this question.

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